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Soybean transpiration, vegetative morphology, and yield components following simulated and actual insect defoliation

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SOYBEAN TRANSPIRATION, VEGETATIVE MORPHOLOGY, AND YIELD COMPONENTS FOLLOWING SIMULATED AND ACTUAL INSECT DEFOLIATION

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Soybean transpiration, vegetative morphology, and yield components following simulated and actual insect defoliation

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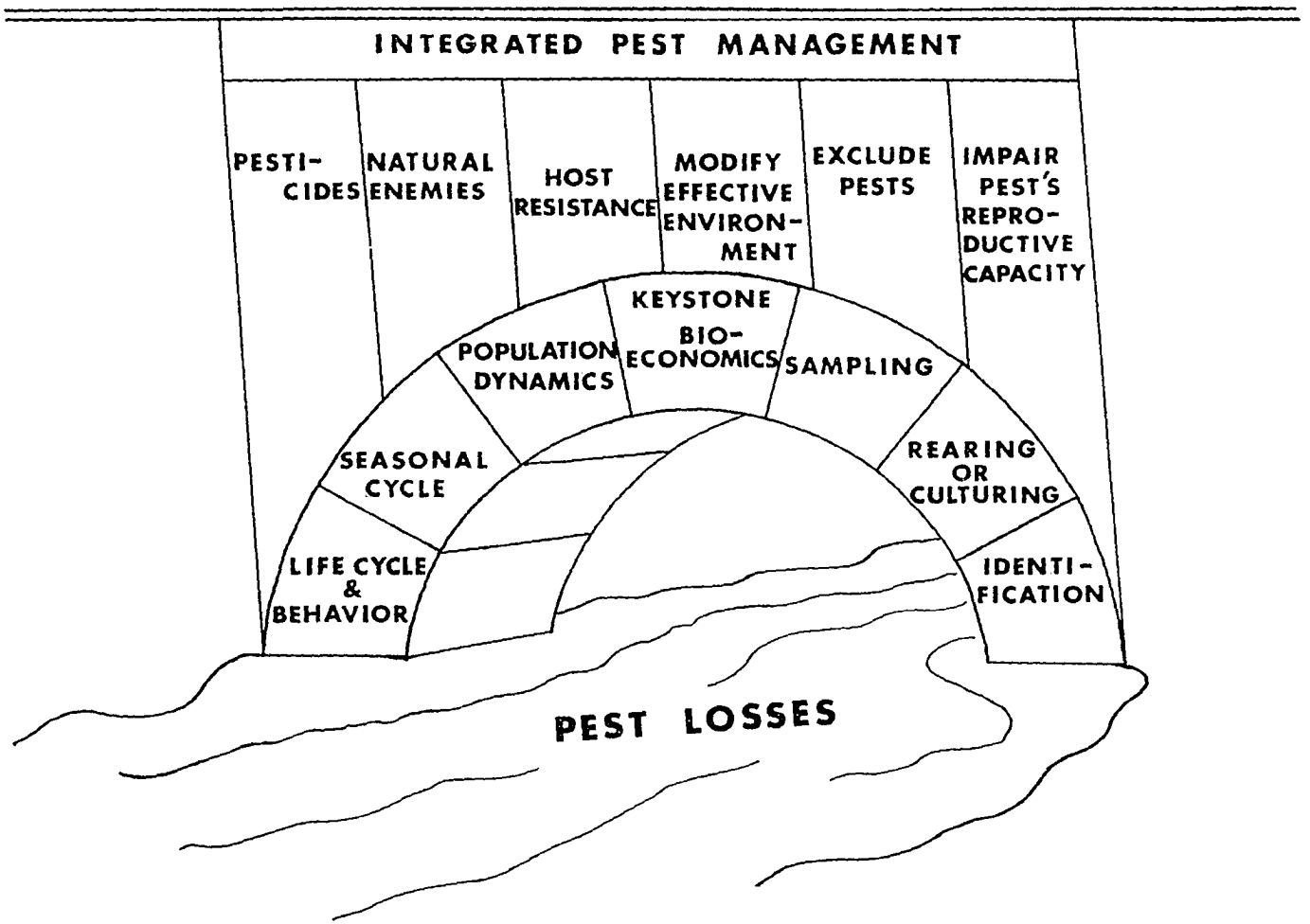
INTRODUCTION

The goal of insect pest management is the maintenance of pest populations at levels which avoid economic damage with minimal cost to the producer and minimal detrimental impacts to the environment (NAS, 1969). The avoidance of economic losses to pests through insect pest management is depicted in Figure 1. Reducing pest status to tolerable levels requires an integration of control measures with knowledge of pest biology. Geier and Clark (1961) termed this control concept "protective management of noxious pests" or "pest management" for short. A thorough knowledge of pest biology and how the pest causes economic loss forms the foundation of any pest management program. In Figure 1, the arch supporting the bridge illustrates areas of pest biology and associated research tools requisite to the development of pest management programs. Available management tactics can then be integrated with this foundation to produce a unified program. The keystone to insect pest management is the relationship between pest biology and the economics of losses and control measures, viz., the realm of bioeconomics.

The economic injury level (EIL), and related concepts of economic damage and economic threshold (ET), characterize the decision-making process in current insect pest management (IPM) programs. These concepts, first defined by Stern et al. (1959), uniquely integrate biology of the crop-pest system and agricultural economics. Economic damage occurs when the amount of injury exceeds the cost of control measures. The EIL is defined as "the lowest population density that will cause economic damage." Because of the time delay between detection of a population exceeding the

Figure 1. A conceptual diagram illustrating how insect pest management integrates available control techniques with an understanding of the insect's life system to reduce pest status [redrawn from Pedigo et al., 1981].


INTEGRATED PEST MANAGEMENT
PESTI-CIDES
NATURAL ENEMIES
HOST RESISTANCE
MODIFY EFFECTIVE ENVIRON-MENT
EXCLUDE PESTS
IMPAIR PEST'S REPRO-DUCTIVE CAPACITY
KEYSTONE BIO-ECONOMICS
POPULATION DYNAMICS
SAMPLING
SEASONAL CYCLE
REARING OR CULTURING
LIFE CYCLE & BEHAVIOR
IDENTI-FICATION
PEST LOSSES

EIL and implementation of control measures, an additional safety margin is required to prevent economic damage. Thus, the ET is defined as the "density at which control measures should be initiated to prevent an increasing pest population from exceeding the economic injury level." In practice, the ET is chosen to prevent the management system from inadvertantly allowing the pest population to exceed the EIL. Both EILs and derived ETs are developmentally dynamic and progress through a series of developmental stages as knowledge of the crop, pest, and their interaction increases (Poston et al., 1983). These stages include: (1) no economic decision criteria; (2) nominal economic decision criteria; (3) calculated economic decision criteria; and (4) comprehensive economic decision criteria. Each step in this developmental sequence represents progress towards greater realism from a managerial perspective. Few crop producers encounter a single pest problem during a growing season. Yet, most nominal and calculated EILs (ETs) are derived for single pest situations. Management decisions for a pest situation should not be made in isolation from other factors affecting crop production. Decisions should incorporate information on the previous and subsequent effects of other crop stressors on yield. As conceptualized by Poston et al. (1983), progress towards comprehensive EILs and ETs can overcome these difficulties.

The heart of an insect pest management program is an understanding of the insect-plant interaction. Traditionally, research efforts in insect pest management have primarily focused on pest population dynamics, sampling programs, development of control alternatives, and the integration of management tactics. Investigations of plant-pest relationships have been

limited, reflecting a lack of cooperative interdisciplinary research and a tendency to treat the plant as an undifferentiated unit. Unfortunately, the "black box" philosophy, while severely impeding progress toward comprehensive EILs, allows the development of calculated EILs. Derivation of the damage-loss relationship can proceed even if the plant is considered a "black box." In contrast, progress towards comprehensive EILs requires a deeper understanding of how insect damage produces yield losses and how other stresses affect the damage-loss relationship.

Quantifying damage-loss relationships provides estimates of crop yield-loss per insect. These estimates form one of the four determinants of the EIL (Stone and Pedigo, 1972). Conventional methods of obtaining these estimates include: observing or manipulating natural insect populations, creating artificial insect infestations, and simulating insect damage (Poston et al., 1983). None of these methods offers a panacea, but each method offers a distinct set of advantages and disadvantages. The choice of method involves careful consideration of pest status, availability of rearing techniques, cropping practices, and the nature of the crop-pest interaction. In the end, experimental resources and logistical considerations may severely limit the range of options available for determining damage-loss relationships.

Although damage authenticity is important, numerous problems arise when manipulating natural or artificial insect populations for damage-loss experiments. Consequently, insect damage is commonly simulated by a variety of methods. Indeed, in some situations, simulation methods provide the only feasible means of determining the damage-loss relationship. Commonly, entomologists have used simulation methods with little regard for

realism in damage appearance, its distribution within the plant, and its distribution through time. Investigators have tacitly assumed that only the quantity of damage affects the plant response and that this response is similar between simulation methods and actual insect damage. Despite widespread usage of simulation methods, these assumptions have largely been unverified. Notable studies comparing simulation methods and actual insect defoliation, such as Poston et al. (1976), Capinera and Roltsch (1980), and Hammond and Pedigo (1981), suggest that simulation methods differ in their fidelity to actual insect damage. Consequently, the damage-loss relationship derived from simulated insect damage should be regarded as an approximation pending the demonstration of its fidelity to actual insect damage (Ingram et al., 1981).

The green cloverworm (GCW) (*Plathypena scabra* [F.]) is considered the most serious soybean pest in the Midwest (Pedigo et al., 1981). Major outbreaks of the GCW in Iowa soybean during 1966, 1968, and 1973, have prompted extensive research on GCW life history, sampling, seasonal population dynamics, and bioeconomics. This research has provided a strong foundation (Figure 1) for subsequent development of a dynamic pest management program. Derivation of EILs for the GCW exemplifies the developmental stages described by Poston et al. (1983). However, continuing progress towards comprehensive EILs requires a more systematic study of soybean response to GCW defoliation. Previous studies exploring the soybean response to defoliation have relied extensively on simulation methods. Although the validity of simulation methods has been examined on excised soybean leaflets for basic physiological processes, data are lacking on how a canopy responds to

simulated and actual insect defoliation. Furthermore, comparative yield responses to different simulation methods have not been investigated.

Therefore, the research presented in this dissertation was designed to elucidate soybean responses to simulated insect defoliation. The GCW in Iowa soybean served as a model for the experimental system. Specifically, the objectives of this research were:

1) To verify the fidelity of simulation methods with actual insect defoliation in terms of canopy transpiration;
2) To detect differences between simulation methods in their effects on soybean transpiration, vegetative morphology, phenological development, yield, and yield components;
3) To characterize soybean response to simulated GCW defoliation and derive general relationships suitable for modeling soybean response to GCW defoliation;
4) To refine current EILs and develop, if possible, more comprehensive EILs for the GCW in Iowa soybean; and
5) To develop a method of incorporating natural mortality estimates into ETs for the GCW in Iowa soybean.

LITERATURE REVIEW

The Green Cloverworm in Iowa

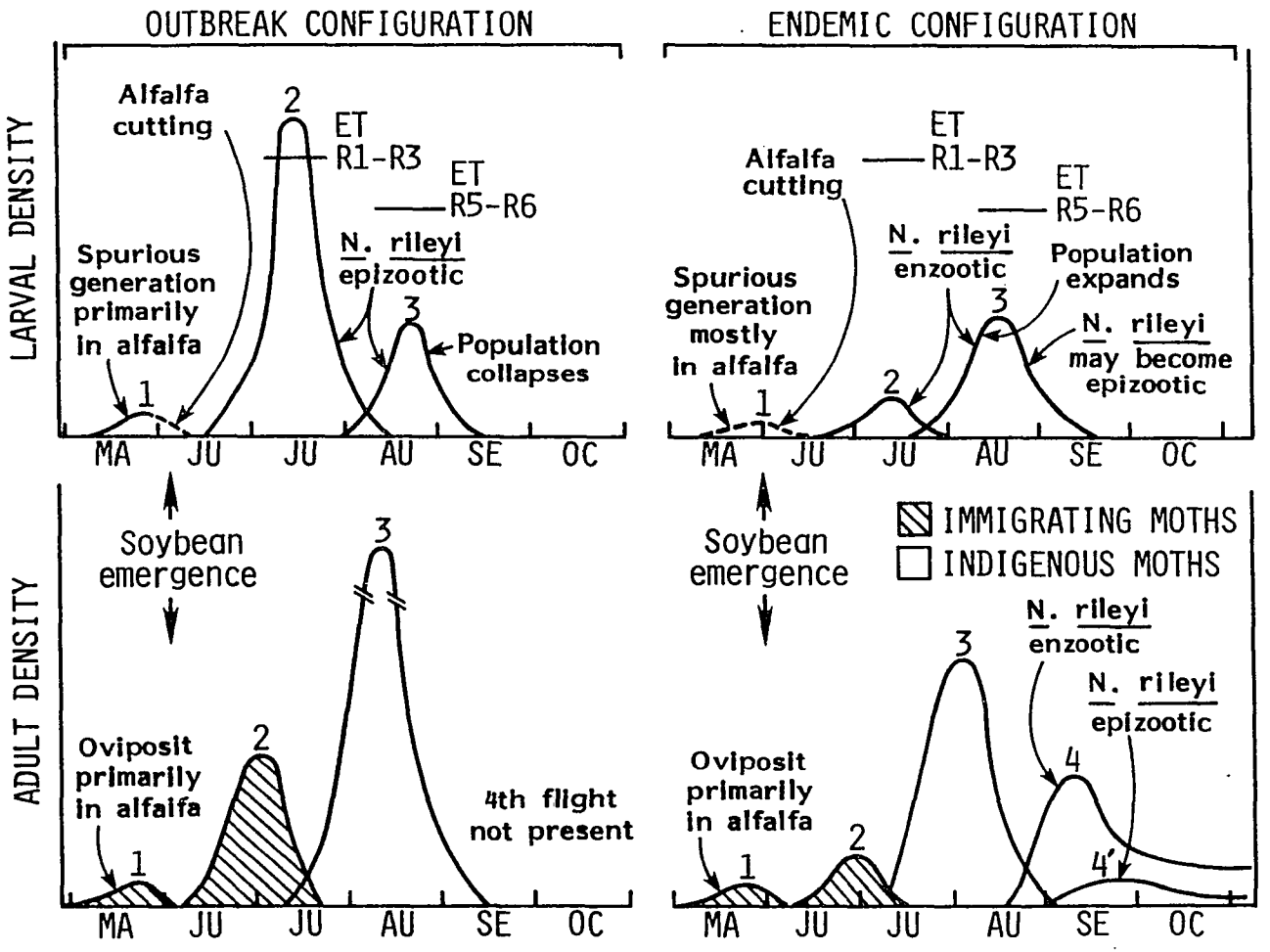
Life history and seasonal phenology

The green cloverworm (GCW) (*Plathypena scabra* [F.]) is a serious but sporadic pest of soybeans throughout the Midwest. Outbreaks occurred in Iowa during 1966, 1968, and 1973, with a number of minor epiphytotics in subsequent years (Pedigo et al., 1983). The random nature of these outbreaks and the extent of subsequent damage has prompted extensive research on GCW life history, sampling, seasonal population dynamics, and impacts on soybean production in Iowa.

The GCW is a noctuid moth with a broad host range of 34 species, including many native and introduced legumes. In the Iowa agroecosystem, its main crop hosts include soybean and alfalfa (Pedigo et al., 1973). Alfalfa management practices in Iowa usually do not permit sufficient thermal units to accumulate between cuttings for complete larval development. Consequently, alfalfa primarily serves as a population sink for GCW with little chance that populations in alfalfa contribute to populations in nearby soybean fields (Buntin and Pedigo, 1983). Because of management practices, populations in alfalfa rarely cause economic loss, but, in soybean, economic losses frequently occur during outbreaks.

Blacklight trap captures of GCW adults indicate that 3 or 4 major flights occur each year in Iowa (Figure 2) (Buntin and Pedigo, 1983). The last flight of each season is composed primarily of dark-phase individuals. These dark-phase adults, in a state of reproductive diapause (Scott and Pedigo, 1977), are the primary overwintering stage in northern latitudes

Figure 2. Idealized phenology and population dynamics of the green cloverworm during outbreak and endemic population configurations in central Iowa soybeans (from Buntin and Pedigo, 1983)


OUTBREAK CONFIGURATION
ENDEMIC CONFIGURATION
LARVAL DENSITY
ADULT DENSITY
Alfalfa cutting
ET R1-R3
ET R5-R6
N. rileyi epizootic
Spurious generation primarily in alfalfa
Population collapses
Spurious generation mostly in alfalfa
N. rileyi enzootic
Population expands
N. rileyi may become epizootic
Soybean emergence
IMMIGRATING MOTHS
INDIGENOUS MOTHS
Oviposit primarily in alfalfa
4th flight not present
N. rileyi epizootic
MA JU JU AU SE OC

(Pedigo et al., 1973; Stone and Pedigo, 1974). Typical Iowa winters are too severe, however, for successful overwintering (Stone and Pedigo, 1974; Myer and Pedigo, 1978). Trends in ovarian development and mating status demonstrate that flight 1 in late May and flight 2 in late June to early July are primarily composed of immigrant adults (Buntin and Pedigo, 1983). Flights of immigrant adults probably originate in the southern United States and migrate northward each spring with suitable synoptic weather patterns. These synoptic weather patterns are probably similar to those patterns which facilitate northward migration of insects such as the potato leafhopper (*Empoasca fabae* [Harris]) (Pienkowski and Medler, 1964) or the black cutworm (*Agrotis ipsilon* [Hufnagel]) (Domino et al., 1983). Within a given year, flight 1 may or may not be detectable. This flight only encounters emergent alfalfa in Iowa during late May and, because of the first alfalfa cutting, few progeny survive to reach adulthood. Flight 2, another immigrant flight in late June, encounters emergent soybeans, and their progeny successfully produce flight 3, the first indigenous flight, in early August. Progeny of this flight in soybean give rise to flight 4, the second indigenous flight, in late August and early September. This flight predominantly contains dark-phase adults in reproductive diapause, which presumably leave the senescing soybeans in search of overwintering sites.

GCW females randomly lay their eggs on the undersides of soybean leaves in the upper canopy (Buntin and Pedigo, 1981). Six larval stages commonly occur with ca. 24% of the larvae requiring a seventh stage to reach pupation (Pedigo et al., 1973). Larvae leave the soybean canopy to pupate in highly littered areas on the soil surface (Bechinski and Pedigo,

1983a). Hammond et al. (1979a) have developed a thermal unit system for predicting development from the egg to adult stages. Development proceeds within a range from 52.0°F to 85.0°F. The cumulative thermal units required to reach each life-stage transition are presented in Table 1.

Table 1. Cumulative thermal units required to reach green cloverworm life-stage transitions (Hammond et al., 1979b)

Life-stage transitions[a]	Cumulative thermal units[b]
Egg → 1st instar	123
1st → 2nd instar	205
2nd → 3rd instar	270
3rd → 4th instar	335
4th → 5th instar	404
5th → 6th instar	473
6th instar → pupa	630
pupa → adult	875

[a]The 6th instar designation includes 7th instars which occur about 24.2% of the time (Stone and Pedigo, 1972).

[b]Thermal units are expressed in Fahrenheit degree-days (base = 52°F).

Two larval generations occur in Iowa soybean each summer (Figure 2). A life-table study completed by Pedigo et al. (1983) has identified two types of population configurations. In the "endemic" configuration, larval densities are subeconomic during both larval generations. Densities during the second generation are larger than those in the first generation (Figure 2). During an "outbreak" configuration, a large immigrant population produces larval densities during the first generation which may be

economically damaging and require control. An epizootic of the entomopathogenic fungus *Nomuraea rileyi* (Farlow) greatly reduces survivorship of second generation larvae. Consequently, densities during the second generation are much smaller than those in the first generation (Figure 2). Thus, the size of the immigrant flight appears to influence stage-specific survivorship. Table 2a presents stage-specific survivorship for the first and second indigenous generations during outbreak and endemic configurations.

Bioeconomics in soybean

Larval GCW defoliate leaves in the upper 1/3 of the soybean canopy (Pedigo et al., 1973). Hammond et al. (1979b) developed a leaf consumption model for this defoliation. The model relates cumulative consumption to cumulative thermal units. The formula derived for this relationship is:

$$Y = 35.33 - 0.25334\,X + 0.00045\,X^2 \quad (R^2 = 0.995),$$

where Y = cumulative leaf consumption per larvae (cm^2) and X = cumulative thermal units measured in Fahrenheit degree-days (base = 52°F).

The impacts of this larval defoliation on soybean production largely depend on the stage of soybean development when defoliation occurs. Studies of soybean response to simulated hail defoliation demonstrate that yield losses vary between stages (Kalton et al., 1949; Camery and Weber, 1953; Fehr et al., 1977). Reproductive stages are more susceptible than vegetative stages. Within reproductive stages, susceptibility of indeterminate soybeans to defoliation peaks during beginning seed (R5) (Fehr et al., 1977). Thus, the relative phenologies of the GCW population and the stage of soybean development play an important role in determining resultant yield-losses. The first larval peak in Iowa soybean usually

Table 2a. Average stage-specific survivorship of green cloverworm life stages in generations I and II during endemic and outbreak population configurations (calculated from Pedigo et al. (1983) and Bechinski and Pedigo (1983))

	Generation I		Generation II	
Life stage	Endemic[a]	Outbreak[a]	Endemic[a]	Outbreak[a]
Egg to small larva	NA[b]	NA	NA	NA
Small to medium larva	.865	.873	.865	.462
Medium to large larva	.326	.292	.326	.100
Large larva to pupa	.574	.515	.719	.284
Pupa to adult	.263	.036	.033	.036
Total generation	.0426	.0047	.0072	.0005

[a]Values for the endemic situation are based on 4 field-years, while values for the outbreak situation are based on 6 field-years.

[b]Data is not available because egg survivorship was not measured in these studies.

coincides with full bloom (R2) to beginning pod (R3). The second larval peak usually occurs when soybeans are in beginning-seed (R5) to full-seed (R6) stages. Despite greater sensitivity of soybean to defoliation at R5, the second larval generation in either population configuration usually does not pose a threat to yield production. During an endemic configuration, although densities are larger in the second generation than in the first generation (Figure 2), both generations fall well below the economic threshold. During years with an outbreak configuration, an epizootic of the entomopathogenic fungus *N. rileyi* causes a collapse of the second larval generation (Pedigo et al., 1983). Consequently, only the first generation of an outbreak configuration possesses the potential to cause economic damage. Caution, however, should be exercised when outbreak configurations coincide with extremely dry conditions. Personal observations during 1983 suggest that, under these conditions, *N. rileyi* may not limit populations during the second larval generation and economic damage may result.

Derivation of economic decision criteria (EILs and ETs) for the GCW has proceeded relatively rapidly through the developmental stages outlined by Poston et al. (1983). Although the GCW was widely recognized as a pest of soybean (Sherman, 1920), no economic decision levels were available to Iowa producers before the 1960s. Establishment of nominal thresholds, 5-10 larvae per 30 cm of row (Stockdale, 1966), coincided with serious outbreaks in Iowa and throughout the Midwest during 1966 (Stone and Pedigo, 1972). These outbreaks also prompted research which established "calculated EILs" for the GCW. Calculated EILs require data on four primary components, including: control costs, crop market value, injury potential per pest

individual, and the relationship between injury to the crop and yield loss. Combining GCW consumption data with the data from agronomic studies on soybean response to simulated hail defoliation (Kalton et al., 1949), Stone and Pedigo (1972) calculated EILs for several stages of soybean development. Later, refinement of these calculated EILs was deemed necessary because hail simulation methods produced damage differing markedly from insect defoliation in its appearance, distribution within the canopy, and its distribution through time. Therefore, Poston and Pedigo (1976), with further modification by Hammond and Pedigo (1982), developed a hole-punching technique for simulating the appearance, vertical canopy distribution, and phenology of GCW defoliation. Fidelity of this damage simulation method, in terms of net photosynthesis and transpiration, has been verified (Poston et al., 1976; Hammond and Pedigo, 1981). Subsequently, this simulation method has been used to refine EILs for first generation GCW larvae (Hammond and Pedigo, 1982; Higgins et al., 1984).

Continuing progress toward the final developmental stage, comprehensive EILs and ETs, requires research on how the abiotic environment and other pest stresses interact with the damage-loss relationship for the target pest. Research on GCW EILs is currently proceeding towards determination of comprehensive EILs, as evidenced by two studies. First, Higgins et al. (1984) explored the interactive effects of GCW defoliation and velvetleaf competition on soybean yield. Additive yield responses in this study suggested that GCW EILs need not reflect the competitive stress of moderate velvetleaf populations. Second, Hammond and Pedigo (1982) documented the effects of drought on the damage-loss relationship and subsequent EILs. Incorporation of moisture stress into comprehensive EILs is

hindered by a lack of data characterizing the damage-loss relationship under normal moisture conditions. Further research is required on the interactions between GCW defoliation and other prominent stress components of the soybean ecosystem, including other insects, weeds, and diseases. If progress toward comprehensive EILs is to succeed, this research must focus on plant response to stress.

Pest management programs

The key element in the operation of a successful pest management program is an accurate, rapid assessment of the pest population's potential for economic damage (Ruesink and Kogan, 1975). Sequential sampling programs are designed to rapidly categorize pest status. Before such programs can be designed, satisfactory sampling techniques must be devised. During the last 10 years, sampling techniques have been devised for each GCW life stage: eggs (Buntin and Pedigo, 1981), larvae (Pedigo et al., 1972), pupae (Bechinski and Pedigo, 1983a), and adults (Pedigo et al., 1982). These sampling techniques have been instrumental in studies on GCW population dynamics and disperson in Iowa soybean. Information on population dynamics is essential to the timing of sequential sampling programs and subsequent management alternatives. Information on insect disperson is one of the primary requisites to constructing a sequential sampling program. Sequential sampling programs for the GCW have concentrated historically on the damaging stage, the larva. Hammond and Pedigo (1976) presented a sequential sampling program for three soybean stages, V5, R2, and R4. This decision-making plan, based on Waters (1966), was derived from limited data that revealed a random disperson. Subsequently, Bechinski et al. (1983)

constructed a decision-making plan from four years of data on larval sampling. This plan was constructed using Iwao's (1975) method, as modified by knowledge of the underlying mathematical distribution, but it does require that sample variance be expressed as a function of mean density. The sequential sampling plan derived by Bechinski et al. (1983) is presented in Table 2b.

Pedigo et al. (1983) found that GCW biotic potential, through immigration, set the stage for population outbreaks and subsequent economic damage. Monitoring the size of immigrant moth flight and categorizing these flights by the subsequent population configuration could prevent unnecessary scouting of soybean fields. For example, if the immigrant flight is small, an endemic configuration would be expected where both larval generations are subeconomic. Scouting for GCW would probably be unnecessary in this situation. This rationale led Pedigo and van Schaik (1984) to develop a new sequential sampling approach, called time sequential sampling. In this article, Pedigo and van Schaik proposed a comprehensive management program involving both time sequential sampling and, if necessary, conventional sequential sampling for GCW larvae.

Soybean Response to Defoliation

Experimental methodology

Defoliators comprise the most abundant and diverse guild of insects that attack soybean in the U.S. (Turnipseed and Kogan, 1976; Pedigo et al., 1982). Therefore, quantifying the relationship between defoliation and yield loss is a fundamental necessity for any insect pest management program in soybean. Quantification of this relationship provides estimates of

Table 2b. Sequential decision plans for GCW larval management in soybeans (Bechinski et al., 1983)

n[b]	Cumulative total no. of GCW larvae[a]											
	Soybean stage V7-R1[c]				Soybean stage R2-R3[d]				Soybean stage R4-R5[e]			
	<		>		<		>		<		>	
	Noneconomic population	Continue sampling		Treatment required	Noneconomic population	Continue sampling		Treatment required	Noneconomic population	Continue sampling		Treatment required
1	---		---		---		---		---		---	
2	---		---		---		---		---		---	
3	37		71		67		113		52		92	
4	53		91		94		146		73		119	
5	68		112		121		179		94		146	
6	84		132		148		212		116		172	
7	100		152		175		245		138		198	
8	117		171		203		277		160		224	
9	133		191		231		309		182		250	
10	150		210		259		341		204		276	

[a]Cumulative number of first- to sixth-stage GCW larvae.

[b]n = number of 60-cm plant shake samples.

[c]V7-R1 = late vegetative to early flower bloom

[d]R2-R3 = late flower bloom to early pod development.

[e]R4-R5 - late pod development to early bean development.

crop yield-loss per insect that are necessary for the calculation of EILs. Conventional methods of obtaining these estimates include: observing or manipulating natural insect infestations, creating artificial infestations, or simulating insect damage. None of these methods offers a panacea; instead, each method possesses its own unique set of advantages and disadvantages. The choice of method involves careful consideration of pest status, availability of rearing techniques and facilities, cropping practices, and the nature of pest injury to the crop. Ultimately, experimental resources and logistical considerations may severely limit the range of available options.

A primary advantage of working with actual insects is the authenticity of the resulting damage. The manipulation of insect populations (artificial or natural) can present tremendous problems. For example, damage levels are hard to control. Even when damage levels can be quantified, relating these levels to a specific insect density may be impossible because of natural mortality and establishment problems. Furthermore, cages designed to contain insects within plots or to exclude natural mortality agents may alter the plant response to insect damage. Hammond and Pedigo (1982) and Higgins et al. (1984) discuss, in greater detail, the difficulties of working with insect problems. Because of these problems, few studies (<14%) have investigated soybean response to defoliation using actual insects. A large proportion of these studies (ca. 50%) have failed to demonstrate significant yield reductions because of establishment or methodology problems (e.g., Mueller and Engroff, 1980; Huffman and Mueller, 1983). Successful studies have primarily relied on insecticides to generate different population levels and, thus, different damage levels

(Heinrich and da Silva, 1975; Ingram et al., 1981). These studies quantified the damage level (reduction in leaf area) that each treatment produced. However, the relationship between insect numbers and resulting damage levels was not quantified.

Because of the difficulties of working with actual insects (or other defoliating agents), a majority of successful studies (>92%) have used methods simulating insect defoliation of soybean. Simulation methods possess many advantages over the use of actual insect damage. Damage levels, the distribution of damage within the canopy, and the distribution of damage through time can be precisely imposed with simulation methods. Moreover, damage levels can be easily replicated from plot to plot and from year to year. Consequently, simulation methods may provide a better experimental tool than actual insect defoliation in assessing soybean response to defoliation. Indeed, simulation methods may provide the only reliable or feasible means of determining the damage-loss relationship in many situations.

Defoliation of soybeans by insects, such as the GCW, has been simulated by a variety of methods. Simulation methods actually involve several components. These components include: defoliation technique (the way in which leaf area is removed), temporal pattern (the distribution of defoliation through time), and the distribution of damage within the soybean canopy. A categorization of the simulation method components used in recent studies of soybean defoliation is presented in Table 3. A wide variety of technique are used to remove leaf area. These techniques include: (1) picking entire leaflets (Todd and Morgan, 1972); (2) cutting off terminal portions of leaflets (Caviness and Thomas, 1980); (3) combinations

Table 3. Categorization of simulation methods used in studies of soybean response to defoliation by their components: defoliation technique,[a] temporal pattern, and damage distribution within the canopy

Component	Prevalence (%)
Technique (n=28)[b]	
Pick	64.3
Punch	10.7
Terminal cut	10.7
Longitudinal cut	3.6
Combination	10.7
Temporal pattern (n=29)	
One-day	75.9
Insect-model	10.3
Sequential	13.8
Damage distribution (n=26)	
Uniform	84.6
Stratified	15.4

[a]Survey based on the following studies (n=28): Fuellman (1944), Kalton et al. (1949), Camery and Weber (1953), Weber (1955), McAlister and Krober (1958), Gould (1960), Begum and Eden (1965), Rosas (1967), Hammerton (1972), Todd and Morgan (1972), Turnipseed (1972), Thomas et al. (1974), Enyi (1975), Ramiro and Oliveira (1975), Teigen and Vorst (1975), Egli and Leggett (1976), Poston and Pedigo (1976), Thomas et al. (1976), Fehr et al. (1977), Lockwood et al. (1977), Hinson et al. (1978), Thomas et al. (1978), Mundhe et al. (1979), Caviness and Thomas (1980), Fehr et al. (1981), Hammond and Pedigo (1982), Higgins et al. (1983), Higgins et al. (1984)

[b]The total number of studies for each component varied from n=28 because multiple papers reported results from the same experiment and some studies experimented with multiple forms of each component.

of cutting terminal portions and picking entire leaflets (Turnipseed, 1972); (4) cutting off lateral portions of leaflet blades (Rosas, 1967); and (5) punching holes in leaflets (Higgins et al., 1983). Most studies have used the leaflet-picking technique because incremental amounts of defoliation (0, 33, 67, 100%) are easily accomplished. In contrast to the variety of defoliation techniques, the last two components, possibly of great importance, have been simplified in most defoliation studies. Defoliation is typically imposed uniformly throughout the canopy on one day. This combination of temporal pattern and damage distribution is atypical of most situations involving insect defoliation of soybean. Consequently, recent studies on one insect pest, the GCW, have closely mimicked the temporal pattern and canopy distribution of its defoliation (Poston and Pedigo, 1976; Hammond and Pedigo, 1982; Higgins et al., 1983). Thus, a wide range of simulation methods are available for examining soybean response to defoliation, but these methods differ widely in their realism towards insect defoliation. Although simulation methods provide a valuable tool for approximating damage-loss relationships, the validity of the derived relationship depends upon the fidelity between the crop's response to simulated and actual insect defoliation.

Traditionally, simulation methods have been used with little regard for realism in either damage appearance, damage distribution within the plant, or damage distribution through time. Consequently, the damage produced by simulation methods often bears little resemblance to actual insect defoliation. This discrepancy has prompted hesitation regarding the fidelity of simulated insect defoliation to actual insect defoliation. Investigators using simulation methods have tacitly assumed that only the

quantity of leaf area removed is important and that soybean response to defoliation does not differ between actual and simulated insect defoliation. Despite the widespread use of simulation methods, the validity of the assumptions has been largely untested. Studies of basic physiological processes, such as transpiration (Hammond and Pedigo, 1981) and net photosynthesis (Poston et al., 1976), have examined soybean response to simulated and actual insect defoliation. These experiments revealed differential effects between some techniques and actual insect defoliation. For example, Poston et al. (1976) reported that defoliation techniques that involved cutting the midvein stimulated net photosynthesis of remaining leaf tissue. In contrast, punching holes in leaves or cutting lateral portions off leaflets produced net photosynthetic rates equivalent to insect feeding. Similarly, Hammond and Pedigo (1981) found that water loss from insect-defoliated leaves exhibited greater similarity in water loss to punch-defoliated leaves than to pick-defoliated leaves. Both of these studies involved excised leaflets. The soybean canopy, however, does not function as a collection of isolated leaflets, but as an integral unit. Therefore, data are lacking that evaluates the comparative responses of a soybean canopy to actual and simulated insect defoliation. Data are also lacking on the relative importance of temporal pattern and damage distribution in their effects on basic physiological processes. More importantly, the question of fidelity between simulated and actual insect defoliation remains unanswered for yield and yield components.

General features of the defoliation syndrome

Soybean response to defoliation caused by a number of natural agents has been extensively researched. These studies have examined the effects of damage simulating defoliation by hail (Kalton et al., 1949; Camery and Weber, 1953; Fehr et al., 1977), insects (Todd and Morgan, 1972; Thomas et al., 1974; Hammond and Pedigo, 1982), and disease (Lockwood et al., 1977) on soybean growth and yield. The collection of soybean responses to defoliation injury is termed the defoliation syndrome. In the following paragraphs, the extensive literature on this topic will be condensed to illustrate a few general principles about the defoliation syndrome in soybean.

Early studies using hail simulation illustrated soybean's amazing compensatory abilities and its varying susceptibility to defoliation at different stages of development. Defoliation during vegetative stages, unless extreme (approaching 100%), rarely resulted in detectable yield loss (Kalton et al., 1949; Camery and Weber, 1953). In contrast, susceptibility to defoliation increased during reproductive stages. Fehr et al. (1977, 1981), using 100% defoliation at all reproductive stages, demonstrated that both indeterminate and determinate soybean are maximally susceptible to defoliation during the beginning seed stage (R5). Susceptibility increased from R2 to R5 and decreased from R5 to R7 (Fehr et al., 1977).

Defoliation has a greater impact on determinate than indeterminate varieties at all stages of reproductive development (Fehr et al., 1977, 1981). Differences in susceptibility seem related to developmental characteristics of determinate and indeterminate varieties. Once flowering began, determinate varieties exhibited less ability than indeterminate

varieties to compensate for defoliation through the addition of new leaf area. For example, indeterminate varieties defoliated 100% during reproductive stages eventually produced 37 to 49% of the leaf area in the undefoliated control plants. In contrast, determinate varieties after 100% defoliation developed only 14 to 27% of the leaf area in their undefoliated control plants. Despite an absolute difference in yield, both determinate and indeterminate varieties exhibited a similar susceptibility relationship between reproductive stages (Fehr et al., 1977, 1981).

The effects of defoliation on yield can be understood more completely by examining its impacts on yield components. Yield represents the end product of several processes: pod set, seed set, and seed fill. Examining the end points of these processes, namely, pod number, seeds per pod and seed size (seed weight), elucidates how yield reductions occur. The relationships between yield and yield components is illustrated in the formula:

$$\text{Yield (g)} = \text{pod number} \times \text{seeds per pod} \times \text{seed size (g)}. \qquad (1)$$

Thomas et al. (1976) found that pod number decreased as defoliation level increased and that the effect on pod number decreased with reproductive maturity. Caviness and Thomas (1980) reported no detectable differences in seeds per pod. Consequently, trends in seed number generally reflected the same relationship with defoliation and stage of reproductive development as pod number. Reductions in seed number after defoliation at different stages parallelled yield reductions (Fehr et al., 1977, 1981). For example, both yield and seed number exhibited greatest sensitivity to defoliation during beginning seed (R5). The response of seed size to defoliation,

like pod and seed number, varied between developmental stages. Defoliation during vegetative stages slightly increased seed size, whereas defoliation during reproductive stages decreased seed size (Kalton et al., 1949). Seed size exhibited the same pattern of stage susceptibility as yield and seed number (Fehr et al., 1977, 1981).

Defoliation affects both pod set and seed fill. The relative importance of defoliation effects on these two yield components has been debated. Early researchers, such as Turnipseed (1972), emphasized the correlation between yield reductions and decreased seed size. Todd and Morgan (1972) reported a similar correlation but concluded that seed size alone could not account for the total reduction in yield. Consequently, they surmised that pod numbers must be affected. Fehr et al. (1977, 1981) demonstrated that both seed number and seed size were reduced by defoliation. Moreover, the percent reduction in seed number exceeded the present reduction in seed size for all reproductive stages except R6. As reproductive development progressed, the effect on seed size accounted for an increasing proportion of the yield reduction.

Other factors may modify soybean response to defoliation, such as moisture stress or previous defoliation. Turnipseed (1972) suggested that defoliaton produces greater absolute yield reductions under the high production levels characteristic of irrigated soybean. Caviness and Thomas (1980) verified that the magnitude of yield reductions after defoliation was greater under irrigated conditions than under nonirrigated conditions. These yield reductions, however, were proportionally equivalent and no interactions between defoliation, stage, and irrigation were detected. Yield reductions from defoliation are enhanced by previous defoliation, but yield

effects definitely are not additive (Gould, 1960; Turnipseed, 1972; Todd and Morgan, 1972). Thomas et al. (1978) demonstrated that sequential defoliations could combine to produce detectable yield losses even though single defoliations did not produce a detectable loss.

Seed quality demonstrated amazing resilience to defoliation. Oil content was decreased by defoliation only when severity exceeded 80% (Kalton et al., 1949; Camery and Weber, 1953; McAlister and Krober, 1958). Iodine number, however, increased at lower levels of defoliation. Protein content after defoliation exhibited variable results. Kalton et al. (1949) reported no detectable differences. McAlister and Krober (1958) and Camery and Weber (1953) reported that protein content was reduced by severe defoliation (>80%). Thomas et al. (1976) also reported significant differences, but these differences were not consistently related to either defoliation level or developmental stage when defoliated.

Defoliation produced differential effects on date of soybean maturity, height at harvest, and lodging susceptibility. The effects of defoliation on date of soybean maturity varied, depending on the stage when defoliation occurred. Moderate to severe defoliation during vegetative stages and early reproductive stages (R1, R2, and R3?) delayed maturation. In contrast, the same levels of defoliation hastened maturation during later reproductive stages (R5 to R7) (Kalton et al., 1949; Camery and Weber, 1953; Fehr et al., 1977; Hinson et al., 1978). Defoliation reduced the stature of indeterminate soybeans at all stages of soybean growth, particularly during vegetative and early reproductive stages (R1 to R2) (Kalton et al., 1949; Camery and Weber, 1953). Although similar reduction in height was observed with a northern determinate variety (Fehr et al., 1981), no height

reductions have been reported for defoliation of southern determinate varieties. Defoliation also reduced the susceptibility of soybeans of both determinate and indeterminate varieties to lodging (Kalton et al., 1949; Fehr et al., 1977; Fehr et al., 1981). Reduction in lodging susceptibility may involve both reduced stature and reduced leaf area to catch the wind's force.

Defoliation syndrome during full bloom and beginning pod

The GCW primarily poses an economic threat to Iowa soybean producers during the first larval generation of an outbreak configuration. This larval generation usually occurs in local fields during full bloom and beginning seed (stages R2 and R3). Therefore, the synthesis and quantitative summarization of data on soybean response to defoliation during these stages was of particular importance to this dissertation.

Fourteen studies have examined defoliation effects on soybean during stages R2 and R3. Unfortunately, data from Turnipseed (1972) and Begum and Eden (1965) were excluded from analyses because their stage descriptions were incomplete or too general. Proper stage identification is essential to the understanding of soybean response to defoliation (Hinson et al., 1978). Data from determinate varieties (5 studies) were analyzed separate from indeterminate varieties (10 studies) because determinates exhibit greater susceptibility to defoliation than indeterminates (Fehr et al., 1981). Among studies on indeterminate varieties, data derived from picking leaflets on one day were analyzed separately from data derived from punching holes over a 12-day period. The results of these regression analyses are presented in Table 4. In all cases, regression equations

Table 4. Linear regressions of soybean yield reductions (%) on defoliation severity (% reduction in leaf area) for determinate and indeterminate soybeans at full bloom (R2) and beginning seed (R3)

Stage	Method[a]	Equation	n	p	R^2
		Determinate			
R2	Pick	% yield loss = .3086 (% defoliation)	24	.0001	.798
R3	Pick	% yield loss = .5150 (% defoliation)	3	.0506	.901
		Indeterminate			
R2	Pick	% yield loss = .2528 (% defoliation)	16	.0001	.895
R3	Pick	% yield loss = .3487 (% defoliation)	8	.0016	.779
R2/R3	Punch #1[b]	% yield loss = .4487 (% defoliation)	17	.0001	.720
R2/R3	Punch #2	% yield loss = .7149 (% defoliation)	6	.0012	.870

[a] "Pick" designates the picking or cutting of leaflets on one day. "Punch" designates punching holes in leaflets according to an insect-consumption model over a 12-day defoliation period.

[b] #1 - Equation determined with data from normal growing conditions. #2 - Equation determined with data from drought conditions.

without an intercept, which pass through the point (0,0), demonstrated the best fit. Results from pick defoliation on one day of both determinate and indeterminate varieties fit the general patterns discussed in the previous section. Soybeans, both determinate and indeterminate, were more susceptible to defoliation during stage R2 than during stage R3. Determinate soybeans also were more susceptible to defoliation at both reproductive stages than indeterminate soybeans.

Simulation method also seemed to have a significant effect on the response of indeterminate soybeans to defoliation. Punch defoliation

following an insect-model temporal pattern (e.g., Hammond and Pedigo, 1982) was more detrimental to yield production than pick defoliation on one day (e.g., Todd and Morgan, 1972). These two simulation methods differ in both technique and temporal pattern. If defoliation technique did not produce differential effects, then defoliation over portions of two stages (R2 and R3) should produce a yield reduction intermediate between one-day defoliation at stages R2 and R3. Instead, the yield reduction for punch x insect-model defoliation exceeded the yield reductions for pick x one-day defoliation at both reproductive stages. This finding suggests that the punch defoliation technique exerts a greater detrimental effect than the pick technique. The relative importance of technique and temporal pattern cannot be resolved from these data. Both components may contribute to the differential effects of simulation methods on yield. Thus, the assumption that simulation methods elicit soybean responses equivalent to insect defoliation may not be valid. Research verifying or disproving the fidelity of simulation methods and evaluating the relative importance of their components (technique and temporal pattern) is required.

The importance of abiotic factors, such as moisture stress, to the damage-loss relationship is suggested by two equations in Table 4 (Punch #1 and #2). Both sets of experiments utilized the same simulation methods and variety and were conducted in the same locale. The only major difference between experiments was the climatic conditions. Data for equation #2 were gathered under moderate to extreme drought stress, whereas the data for equation #1 were obtained under normal moisture conditions. Drought stress clearly accentuated the detrimental effects of defoliation.

Yield reductions after defoliation at stages R2 to R3 involve reductions in both pod or seed number and seed size (Thomas et al., 1976; Fehr et al., 1977; Caviness and Thomas, 1980). Reductions in pod or seed number are proportionately greater than the reduction in seed size. For example, 100% defoliation at R2 reduced seed number 13%, whereas it reduced seed size only 3% (Fehr et al., 1977). This example illustrates the concept that defoliation exerts a stronger effect on immediate processes than on later processes. At stages R2 and R3, pod set is occurring. Thus, it is not surprising that pod and seed number are reduced more than seed size.

Defoliation affects more than yield and yield components. Height, maturation, and lodging susceptibility also are affected by defoliation at stages R2 and R3. Height is reduced by defoliation and the degree of height reduction increases with defoliation level (Kalton et al., 1949; Weber, 1955; Teigen and Vorst, 1975). Defoliation delays maturation of soybean defoliated at R2 and R3, if defoliation levels are severe (approaching 100%) (Kalton et al., 1949; Camery and Weber, 1953; Weber, 1955). For example, 100% defoliation at R2 delayed the maturity of two indeterminate varieties six days (Fehr et al., 1977). Finally, although lodging susceptibility generally declines with defoliation severity at all reproductive stages, the greatest reductions seem to occur in early reproductive stages, such as R2 and R3 (Walker, 1971; Fehr et al., 1977). Higgins et al. (1983) contend that this reduction in lodging susceptibility is an important part of the defoliation syndrome. Furthermore, this change in lodging susceptibility may partially offset the detrimental effects of defoliation.

A Critical Evaluation of Simulated Damage Experiments

The process of synthesizing the available literature on soybean response to defoliation has pointed out the pitfalls and shortcomings of previous research on this topic. Moreover, this literature review has demonstrated the need for a critical evaluation of defoliation studies and the presentation of suggestions for future researchers.

Perhaps the greatest impediment to the appropriate use of simulation methods in soybean entomology is the legacy left by hail simulation studies. The use of methods simulating insect defoliation originated in hail simulation studies. Despite drastic differences in the damage characteristics of hail and insects, entomologists have persisted in their employment of methods simulating hail defoliation. The use of hail simulation methods to mimic insect defoliation is inappropriate for several reasons. First, the fidelity of hail simulation techniques to actual insect defoliation is questionable. Hail simulation typically involves picking entire leaflets uniformly throughout the canopy on one day. In contrast, insect defoliation usually produces holes in leaflets, is restricted in its distribution within the canopy, and occurs over a period of several days to weeks. Intuitively, simulation methods should approximate insect defoliation as closely as possible in appearance, distribution within the canopy, and distribution through time. Discrepancy in any one of these components of damage simulation could affect the resultant damage-loss relationship. Therefore, an important step in the use of any simulation method should be a verification of its fidelity to actual insect defoliation. Despite widespread use of hail simulation methods, its fidelity to insect defoliation has not been examined. Second, the purpose of hail simulation studies is

to quantify yield reductions for insurance purposes. Consequently, the damage levels of interest in hail studies extend from 0 to 100%. From a pest management standpoint, it is more important to characterize the damage-loss relationship at lower defoliation levels. The purpose of quantifying the damage-loss relationship is to detect when economic loss occurs. The scale of interest to entomologist ranges from 0 to perhaps a maximum of 30% during reproductive stages. Yet, a majority of studies (ca. 75%) have not included defoliation levels below 33%. Consequently, despite an abundance of studies, the relationship between economic damage and percent defoliation is poorly quantified. Third, hail simulation has focused on soybean response at discrete stages, whereas insect defoliation occurs over a period of time, spanning more than one plant stage. A basic problem exists in translating defoliation over time into percent defoliation at a distinct plant stage. In addition, information on the additivity of damage during different plant stages is lacking. Finally, the focus on realized damage (% defoliation) rather than on potential damage (insect numbers) prevents the formation of true economic thresholds. In conclusion, persistent use of hail simulation methods is largely a matter of convenience and has tended to minimize our understanding of (1) plant response to insect defoliation and (2) the relationship between insect numbers and economic damage.

The development of comprehensive EILs requires more than a documentation of damage-loss relationships. The key to deriving comprehensive EILs is understanding the plant, how insect defoliation affects it, and how other stresses modify the relationship between insect defoliation and yield

loss. Unfortunately, most studies on soybean response to defoliation have concentrated solely on yield. Information on how defoliation affects other features, such as vegetative morphology, yield components, and basic physiological processes, is lacking or fragmentary. The relative lack of interest in these areas is demonstrated by the survey in Table 5. For example, few studies have examined the effects of defoliation on leaf area (ca. 30%). Yet, remaining leaf area and its ability to intercept light may explain most of the yield consequences of defoliation (Hinson et al., 1978; Fehr et al., 1981; Ingram et al., 1981). Clearly, if our understanding of soybean response to defoliation is to advance appreciably, the "black box" approach must be abandoned. Research must focus on the plant and how insect defoliation produces yield reductions.

Table 5. Survey of vegetative and reproductive parameters reported from studies examining soybean response to artificial defoliation[a]

Parameter	Prevalence (%)
Vegetative	
Leaf area	30.8
Vegetative development	3.8
Reproductive development	3.8
Branching	3.8
Height	23.1
Lodging	19.2
Maturity	23.1
Reproductive	
Yield	100.0
Total plant weight	7.7
Apparent harvest ratio	3.8
Pod number	42.3
Seed number	26.9
Seeds per pod	11.5
Seed size	53.8
Seed quality	23.1

[a]Survey based on the following studies (n=28): Fuellman (1944), Kalton et al. (1949), Camery and Weber (1953), Weber (1955), McAlister and Krober (1958), Gould (1960), Begum and Eden (1965), Rosas (1967), Hammerton (1972), Todd and Morgan (1972), Turnipseed (1972), Thomas et al. (1974), Enyi (1975), Ramiro and Oliveira (1975), Teigen and Vorst (1975), Egli and Leggett (1976), Poston and Pedigo (1976), Thomas et al. (1976) Fehr et al. (1977), Lockwood et al. (1977), Hinson et al. (1978), Thomas et al. (1978), Mundhe et al. (1979), Caviness and Thomas (1980), Fehr et al. (1981), Hammond and Pedigo (1982), Higgins et al. (1983), Higgins et al. (1984).

PART I. WATER LOSS FROM SOYBEAN FOLLOWING SIMULATED AND ACTUAL INSECT DEFOLIATION

ABSTRACT

Soybean water-loss following defoliation was investigated in two experimental systems, excised leaves and field-grown potted plants. Transpiration from excised leaves increased following defoliation as a linear function of cut edge per leaf. In contrast, transpiration from soybean canopies decreased following defoliation by two lepidopteran defoliators, the green cloverworm (*Plathypena scabra* [F.]) and the cabbage looper (*Trichoplusia ni* [Hübner]), and two simulation methods, punching holes in leaflets and picking entire leaflets. Cut leaf edge, an important determinant of water loss from excised leaves, only increased water loss in the first 16 hours postdefoliation. Defoliation methods also produced transitory differences in transpiration rates during the first 16 hours after defoliation. These differences seemed related to the "hole" characteristics produced by the methods. Total water loss did not differ significantly between methods. Therefore, both punch and pick simulation methods produced acceptable fidelity in soybean water-loss to actual insect defoliation.

defoliation produced by leaf-feeding insects. Consequently, Poston and Pedigo (1976) and Hammond and Pedigo (1982), aiming at greater fidelity to insect defoliation, simulated lepidopteran defoliation by punching holes in leaflets.

Implicit within the choice of any simulation method is the assumption that the defoliation technique will not alter soybean's response to defoliation. Despite widespread use, the validity of this assumption for the leaf-picking technique has not been evaluated. Fidelity of the punch technique to green cloverworm (GCW) (*Plathypena scabra* [F.]) defoliation has been established for basic physiological processes. Poston et al. (1976) found that punch defoliation adequately simulates GCW defoliation based on measurements of net photosynthesis. Hammond and Pedigo (1981) demonstrated that water loss from insect-defoliated leaves exhibits greater similarity to water loss from punch-defoliated than pick-defoliated leaves. Both insect and punch defoliation produce "cut" leaf edges. Increased water loss from punch and insect-defoliated leaves may reflect uncontrolled water loss from exposed leaf mesophyll at these edges (Hammond and Pedigo, 1981). Davidson (1973) hypothesized that uncontrolled water loss from defoliated leaves contributes to yield loss in cotton. Defoliation increases water loss from excised soybean trifoliolates (Hammond and Pedigo, 1981). However, a plant or plant canopy does not function as a collection of isolated leaves, but as an integral unit. Water loss, or transpiration, from this integrated unit depends on incident solar radiation, wind, and the water status of the plant (Bidwell, 1979). Little is known about the transpiration of an entire plant or plant canopy following insect defoliation.

This paper describes the results and implications of two complementary experiments on soybean water-loss following insect defoliation. The objectives of the first experiment were: (1) to determine the relationship between defoliation and water loss from excised leaves; and (2) to assess the contribution of cut leaf edge. The second experiment extended these objectives to functional soybean canopies. The objectives of this second experiment included: (1) determining the relationship between defoliation and water loss from a functional soybean canopy; (2) assessing the contribution of cut leaf edge to overall water loss; and (3) evaluating the fidelity, in terms of water loss, of punch and pick defoliation to defoliation by two insects, the green cloverworm and the cabbage looper (CL) (*Trichoplusia ni* [Hübner]).

MATERIALS AND METHODS

Experiment 1

Measurement of water loss from excised leaves followed the procedure developed by Hammond and Pedigo (1981). At soybean stage V5 (Fehr and Caviness, 1977), trifoliolates from node three of greenhouse-grown plants were excised near the petiole base. The petioles were recut under water and the leaves inserted into florist Aquapics®. Excised leaves were arranged in a randomized complete block design with 15 leaves per block. Within each of the three blocks, leaves were assigned at random to 11 treatments as follows: three leaves to control 1, three leaves to control 2 and one leaf to each of nine defoliation treatments. Defoliation treatments included a factorial combination of three defoliation levels (3, 6, and 9 cm^2) and three punch sizes (cork borer nos. 2, 4, and 8). These cork borers removed different leaf areas per punch (.192, .397, and 1.094 cm^2, respectively) and generated different lengths of cut edge per unit of defoliation (8.1, 5.6, and 3.4 cm/cm^2, respectively). Consequently, removal of equivalent leaf area by each cork borer produced unequal lengths of cut edge.

After defoliation, remaining leaf area per trifoliolate was measured with a LiCor® LI-3000 leaf area meter. Area of the leaves in control 2 was measured upon completion of the experiment. This control was included to assess possible handling effects on subsequent water loss. During the experiment, leaves were maintained under laboratory conditions of ca. 22-24° C, 20-30% RH, and a photophase/scotophase ratio of 15:9. Water loss was monitored over a 48-hour period by regularly recording the water volume

needed to maintain a predetermined level within the aquapics.

Water loss, expressed as $g/m^2/hour$, was analyzed with standard ANOVA techniques. Significant treatment effects were isolated with orthogonal treatment comparisons.

Experiment 2

Water loss from functional soybean canopies was measured using a pot weighing method. This simple method, which predates modern lysimeters, utilizes repeated weighings of potted plants to provide a quantitative determination of transpiration rates (Bidwell, 1979).

Preparation of potted soybean plants

The objective of the following preparations was to produce potted soybean plants morphologically and physiologically similar to field plants. Potted, greenhouse-grown soybean plants differ drastically in morphology from field-grown plants. This change may affect both insect defoliation and plant response. For example, Hammond et al. (1979a) found that GCW consumption of soybean foliage differed significantly between greenhouse and field leaves. Differences in consumption were related to decreased specific leaf weight (g/cm^2) of greenhouse leaves. Therefore, to achieve morphological and physiological similarity to field plants, the potted plants used in this experiment were grown outdoors in a soybean-row environment.

The normal, soybean-row environment was provided by a plot of soybeans (cv. Amsoy 71) measuring 20 m x 16 rows (76 cm row spacing). These soybeans were planted 3 June 1983. In the center eight rows, 100 11.6-liter plastic nursery pots were buried flush with the soil surface at 1-m intervals. Each pot was filled with a 3:1 mixture of field soil and sand.

Soybeans, inoculated with *Rhizobium japonicum* to insure nodulation, were planted 1-2 days after plot establishment. On 10 June 1983, the emerged soybeans were thinned to 26.7 plants per m of row (6 plants per pot). Sethoxydim (.32 kg a.i./ha) plus crop oil concentrate (2.33 liter/ha) was applied, postemergence, to control grass weeds. Bentazon (1.12 kg a.i./ha) plus crop oil concentrate (2.33 liter/ha) was applied, postemergence, to control the broadleaf weeds.

Potential problems with reduced rooting volume were eliminated through irrigation and fertilization. Pots were trickle irrigated to saturation two or three times weekly. Both potash and phosphate fertilizers were thoroughly mixed with the soil in each pot at a rate of 673 kg/ha.

On 25 July 1983, when the pots were removed from the row setting, no differences in vegetative or reproductive development were detected between potted and normal row plants. Therefore, the cultural practices just outlined successfully produced potted plants equivalent to normal field plants.

Rearing of lepidopteran defoliators

The objective of our rearing program was to match the relative phenology of our experimental system, reared GCW and CL larvae on potted soybean, with that of our model system, the GCW on Iowa soybean. Consequently, rearing procedures for the GCW and CL were coordinated to produce ultimate instars on 26 July 1983. This date occurred in a period when natural defoliation by GCW was expected to peak in local soybean fields.

GCW eggs were obtained from feral, immigrant females between 22 June and 1 July 1983. These eggs were held at 4.4°C until 5 July. Larvae then

were reared from these eggs, in batches of 50 larvae per 0.5-liter ice cream carton, following the procedures outlined by Hammond et al. (1979b). Throughout their development, GCW larvae fed on leaves from field soybeans.

CL larvae were obtained from a colony maintained at the Corn Insects Research Laboratory, USDA - ARS, Ankeny, Iowa. The CL larvae were reared on a basic pinto bean diet (Reese et al., 1972), as modified by Cossentine (1982), rather than on leaves from field soybean. Previous experience with this colony indicated that the larvae readily defoliated field soybean with no prior exposure.

Larvae of both species were reared in a Percival CE-2 environmental chamber maintained at 21.1°C, 35-40% RH, and a photophase/scotophase ratio of 14:10.

Experimental procedures

On 25 July 1983, 96 pots were removed from their row environment and transported to a nearby mowed-grass surface. Plant density in each pot was reduced from six to three plants per pot. Thinning was necessary to decrease the rate of water loss from each pot and, thus, extend the period of water loss measurements before soil resaturation was necessary. Soil in each pot was saturated. The plants were allowed to adjust to the experimental environemnt for 24 hours.

Pots were arranged in a randomized complete block design with four replications and 24 treatments. These treatments included a factorial combination of four defoliation methods (GCW, CL, punch, and pick) and six targeted levels of defoliation (0, 16, 32, 48, 64, and 80%). Based on leaf area per pot and a GCW consumption model (Hammond et al., 1979b), GCW

infestation levels necessary to reach these targeted levels were calculated at 0, 15, 30, 45, 60, and 75 larvae per pot, respectively. Because CL larvae were nearing pupation, CL infestation levels were adjusted upwards to 0, 30, 60, 90, 120, and 150 larvae per pot, respectively. Both CL and GCW larvae were introduced at dusk on 26 July 1983 to favor successful establishment. Each pot was surrounded with a cylinder of hardware cloth to prevent larval dispersal. During the afternoon of 27 July, all pick and punch defoliation was performed. In pick defoliated pots, the desired proportion (0, 1/6, 1/3, 1/2, 2/3, 5/6) of leaflets was removed with a razor blade. In punch-defoliated pots, a cork borer with an area of 2.85 cm^2 was used to remove the desired proportion of each leaflet.

When surrogate damage was completed, larvae also were removed from plants receiving insect defoliation. The soil in each pot was saturated with water and the pot nested within two plastic bags. The tops of the plastic bags were sealed around the bases of the soybean plants with duct tape to prevent loss of water vapor from the soil in each pot. Over the short duration of the experiment, any change in plant weight through photosynthesis and respiration was considered negligible. Thus, weight loss of the potted soybean plant system reflected water vapor lost through transpiration. Each pot was weighed at approximately 0, 16, 24, 40, and 48 hours postdefoliation. The transpiration rate for each period was calculated by dividing the change in pot weight by the length of each measurement period. A thunderstorm the night of 28 July, between 24 and 40 hours postdefoliation, prevented accurate measurement for this time period. At 72 hours postdefoliation, the leaves were stripped from each pot and photocopied.

Leaf area per pot was measured with a LiCor® LI-3000 leaf area meter. The length of cut edge per pot was estimated (measured) from the photocopied leaves with a map measurer.

This experiment was designed to evaluate the fidelity of simulated to actual insect defoliation using standard ANOVA analyses. Two factors, however, necessitated an analysis of covariance instead of the ANOVA. First, the defoliation level achieved by any defoliation method was uncontrolled. Consequently, significant differences in leaf area between defoliation methods occurred. Secondly, a strong relationship between remaining leaf area and water loss was detected during each measurement period. Therefore, an analysis of covariance was required to remove the bias produced by differences in leaf area between methods. Cut leaf edge was not used as covariate because pick defoliation did not produce cut leaf edge.

RESULTS AND DISCUSSION

Experiment 1

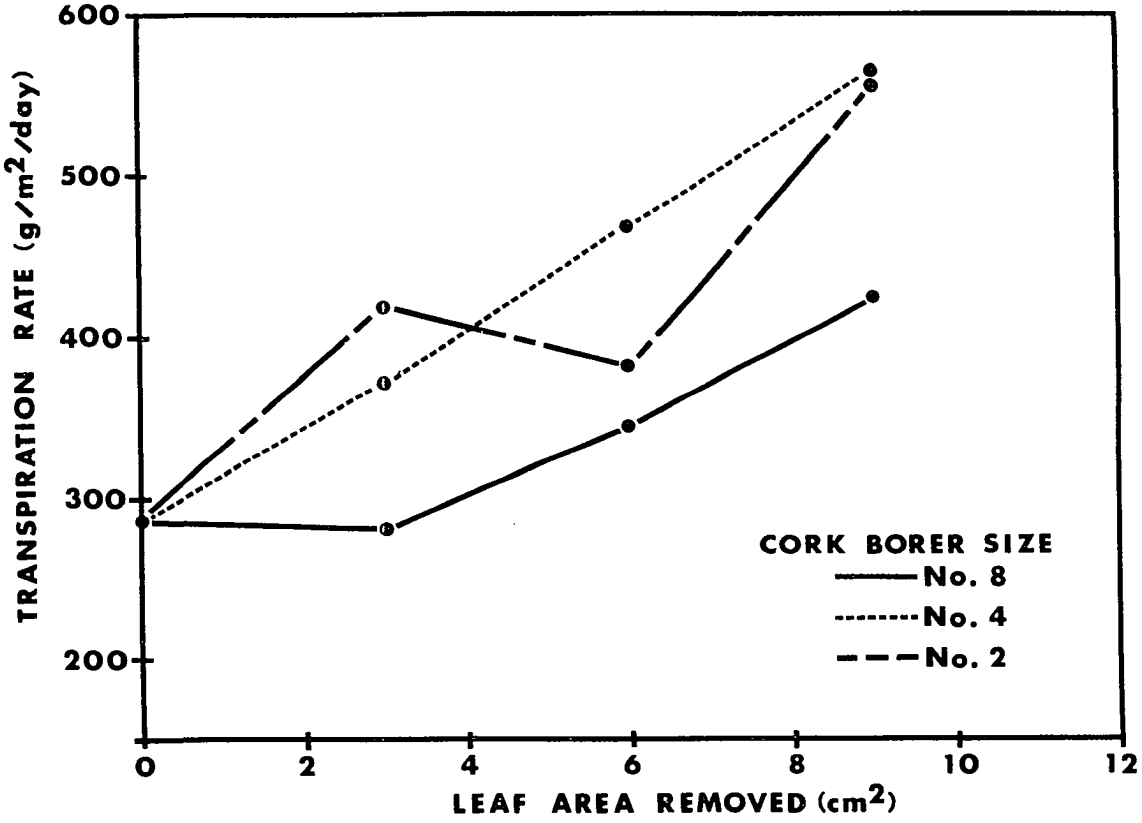
Water loss ($g/m^2/hr$), averaged for each treatment over the entire experiment, is presented in Figure 1. Defoliated leaves lost water at a higher rate than undefoliated leaves ($F_{1,29}=13.13$, $p=.001$). Handling of leaflets did not affect the rate of water loss. Transpiration increased with the amount of area removed ($F_{2,29}=5.72$, $p=.008$). Transpiration from leaves with 3 cm^2 removed was lower than transpiration from leaves with 6 and 9 cm^2 removed ($F_{1,29}=5.61$, $p=.025$). Similarly, leaves with 9 cm^2 removed lost water at higher rate than leaves with 6 cm^2 removed ($F_{1,29}=5.82$, $p=.022$). Overall, water loss increased as a quadratic function of defoliation percentage:

$$\text{Water loss} = .031619 - .000457(\%\ \text{defoliation}) + .000123(\%\ \text{defoliation})^2 \qquad R^2 = .505.$$

Hammond and Pedigo (1981) found a similar increase in water loss from excised soybean leaves after defoliation.

Size of the hole produced by the cork borer also significantly affected water loss ($F_{2,29}=3.57$, $p=.041$) (Figure 1). Leaves defoliated with the largest cork borer (No. 8) transpired less than leaves defoliated by either the No. 4 or No. 2 cork borers ($F_{1,29}=7.05$, $p=.013$). No significant difference was detected between leaves damaged by either the No. 4 or No. 2 cork borers. All interactions between area removed and cork borers were insignificant. No day-by-treatment interactions were significant, indicating that the water loss patterns just discussed were consistent between days.

Figure 1. Water loss from excised soybean leaves after punch defoliation expressed as a function of removed leaf area and cork borer size


600
500
400
300
200
TRANSPIRATION RATE (g/m2/day)
0
2
4
6
8
10
12
LEAF AREA REMOVED (cm2)
CORK BORER SIZE
No. 8
No. 4
No. 2

Increased water loss associated with smaller cork borer size suggested that cut leaf edge was contributing to water loss. The importance of cut edge was assessed by regression of water loss on the length of cut edge. This regression analysis revealed a significant linear relationship between water loss and the length of cut edge per leaf:

$$\text{Water loss} = .030647 + .000325(\text{cut edge}) \qquad R^2=.390.$$

The importance of cut edge, in explaining water loss, is indicated by the fact that the regression relationship accounted for 78% of the treatment variability. These findings support the contention of Davidson (1973) and Hammond and Pedigo (1981) that the cut edges produced during insect or punch defoliation increase water loss. However, a decrease in slope and R^2 from day 1 to day 2 (Figure 2) suggests that a healing response was occurring at these cut edges. If healing occurs, then the effects of cut leaf edge are of transitory importance to the water status of the soybean plant.

Experiment 2

Mean foliage characteristics of soybean plants following actual and simulated insect defoliation appear in Table 1. As indicated by remaining leaf area, methods did not achieve equivalent levels of defoliation. Defoliation by both GCW and CL larvae was less than projected. Many CL larvae entered the prepupal stage during the 24-hour defoliation period. Presumably, handling stress and elapsed time before reestablishment of feeding reduced potential defoliation by both GCW and CL larvae. Punch defoliation was slightly less severe than projected because of a tendency for punchers to overestimate the proportion of leaf area they removed. Despite these

Figure 2. Linear regressions of water loss from excised soybean trifoliolates on the length of cut edge per leaf after defoliation

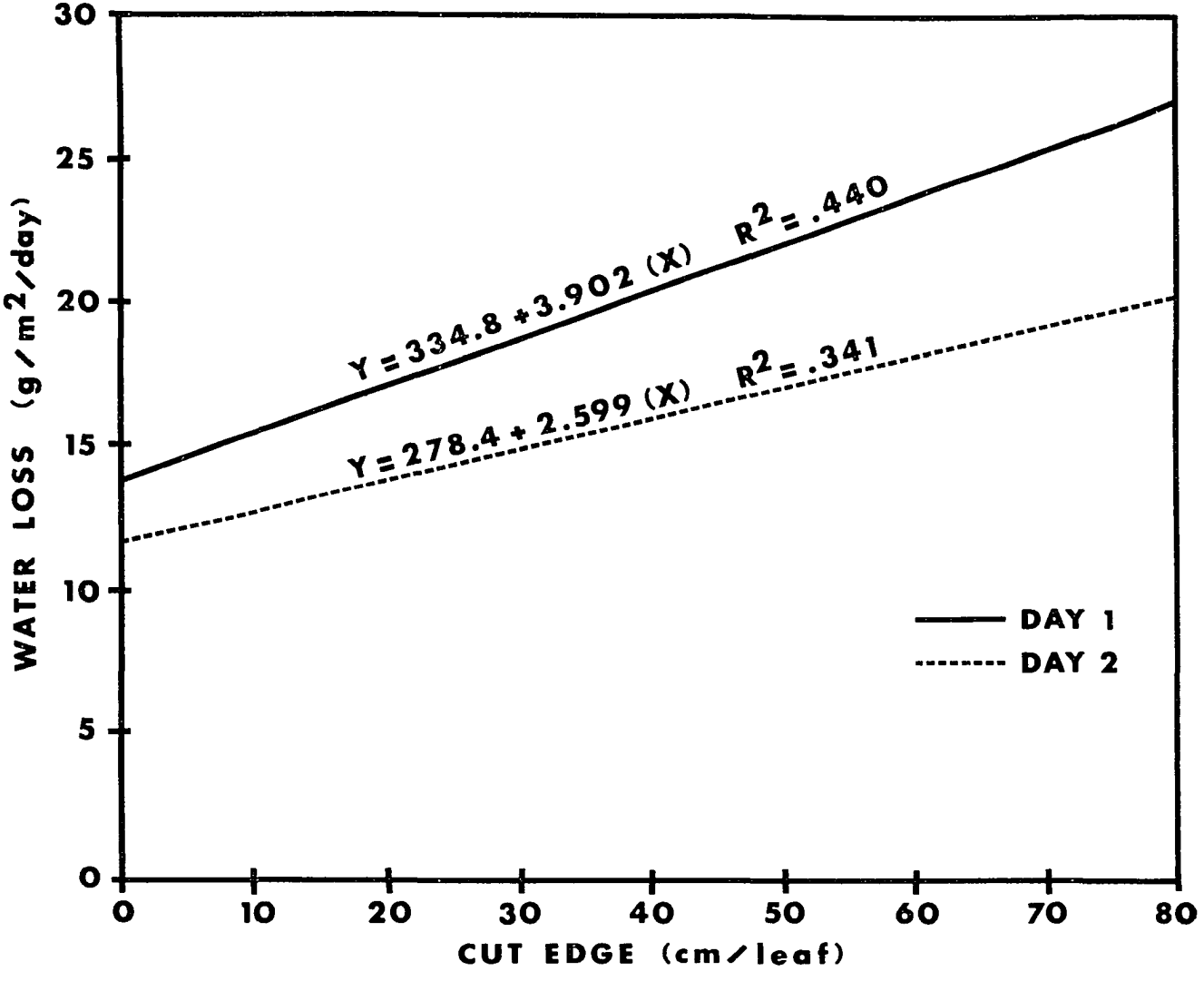

30
25
20
15
10
5
0
WATER LOSS (g/m2/day)
Y = 334.8 + 3.902 (X) R2 = .440
Y = 278.4 + 2.599 (X) R2 = .341
DAY 1
DAY 2
0
10
20
30
40
50
60
70
80
CUT EDGE (cm/leaf)

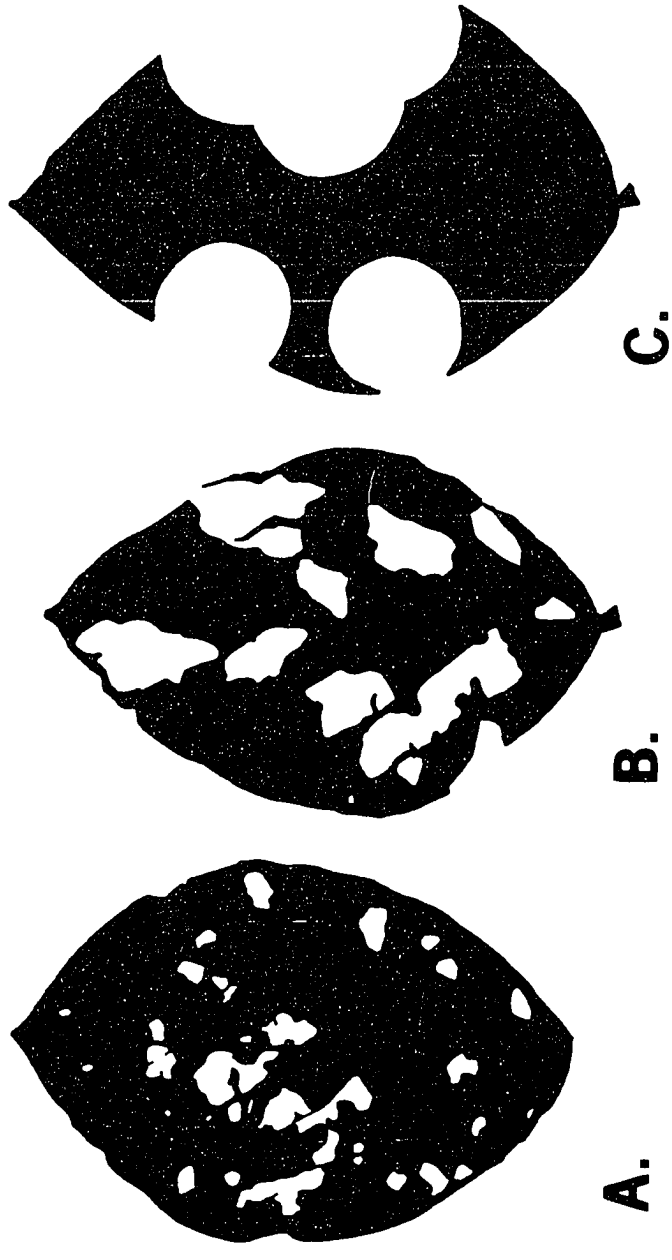
Table 1. Mean foliage characteristics of soybean plants following defoliation by insects and simulation methods

Defoliation treatment	N	Remaining leaf area[a] (cm^2)	Cut edge[a] (cm)	Ratio of cut edge:leaf area	
				Remaining (cm/cm^2)	Removed (cm/cm^2)
Check	13	1823 a	80.2 b	.042 c	--
Green cloverworm	20	1459 b	675.9 a	.520 b	1.857
Cabbage looper	20	1705 ab	669.4 a	.384 b	5.110
Picking leaflets	20	963 c	37.3 b	.041 c	.043
Punching holes	20	1113 c	704.9 a	.749 a	.994

[a]Means followed by different letters are significantly different ($P < 0.05$) by Duncan's Multiple Range Test.

differences in remaining leaf area, GCW, CL, and punch defoliation produced similar lengths of cut edge. Differences in defoliation level but similarities in cut edge suggested a basic difference in the hole characteristics of these defoliation methods. The length of cut edge produced per unit of defoliation provides an indication of average hole size. The importance of this ratio (cut edge/leaf area removed) will be discussed in greater detail later in this paper. Leaflets typifying GCW, CL, and punch defoliation are illustrated in Figure 3. Undefoliated plants possessed small amounts of cut edge because wind slightly tatters leaflets. Naturally, pick defoliation, by removing entire leaflets, decreased cut edge per plant but did not alter the amount of cut edge per unit of remaining leaf area. Because the equivalency, in water loss, of cut petiolules to cut leaf edge is unknown, pick defoliation treatments were excluded from any discussion involving cut edge and its importance to water loss.

Figure 3. Representative soybean leaflets illustrating the appearance of: A. cabbage looper, B. green cloverworm, and C. punch defoliation


A.
B.
C.

The relationship between water loss and remaining leaf area is depicted for each time period (0-16, 16-24, and 40-48 hours postdefoliation) in Figure 4 and Table 2. In each period, water loss increased linearly with remaining leaf area, i.e., decreased with defoliation intensity. Differences in slopes and intercepts of the regression lines between these periods were related to incident solar radiation. As incident solar radiation increased, both slope and intercept increased. Leaf area accounted for a greater proportion of experimental variability under the sunny conditions (.750 langley/min) of period 2 (16-24 hours) than under the partly cloudy conditions (.593 langley/min) of period 3 (40-48 hours) or the dusk to dawn conditions (.153 langley/min) of period 1 (0-16 hours).

During all periods, defoliation reduced water loss. This result directly contradicted predictions from experiments on excised leaves. The results of our first experiment and those of Hammond and Pedigo (1981) suggested that water loss would increase following defoliation. Contradictory results between experiments clearly demonstrate that excised leaves cannot be used to predict canopy performance. Unlike the excised leaf, canopy transpiration is limited by overall plant-water relationships and the stresses of the field environment.

Davidson (1973) and Hammond and Pedigo (1981) suggested that the cut edges produced by defoliation significantly contribute to overall water loss. The results of our first experiment also ascribed an important role to cut leaf edge in postdefoliation water loss, but indicated that a healing response might limit its importance. The relationship between cut leaf edge and water loss from the soybean canopy is indicated by the linear regression coefficients in Table 2. The first value following each

Figure 4. Transpiration from defoliated soybean canopies as a function of remaining leaf area

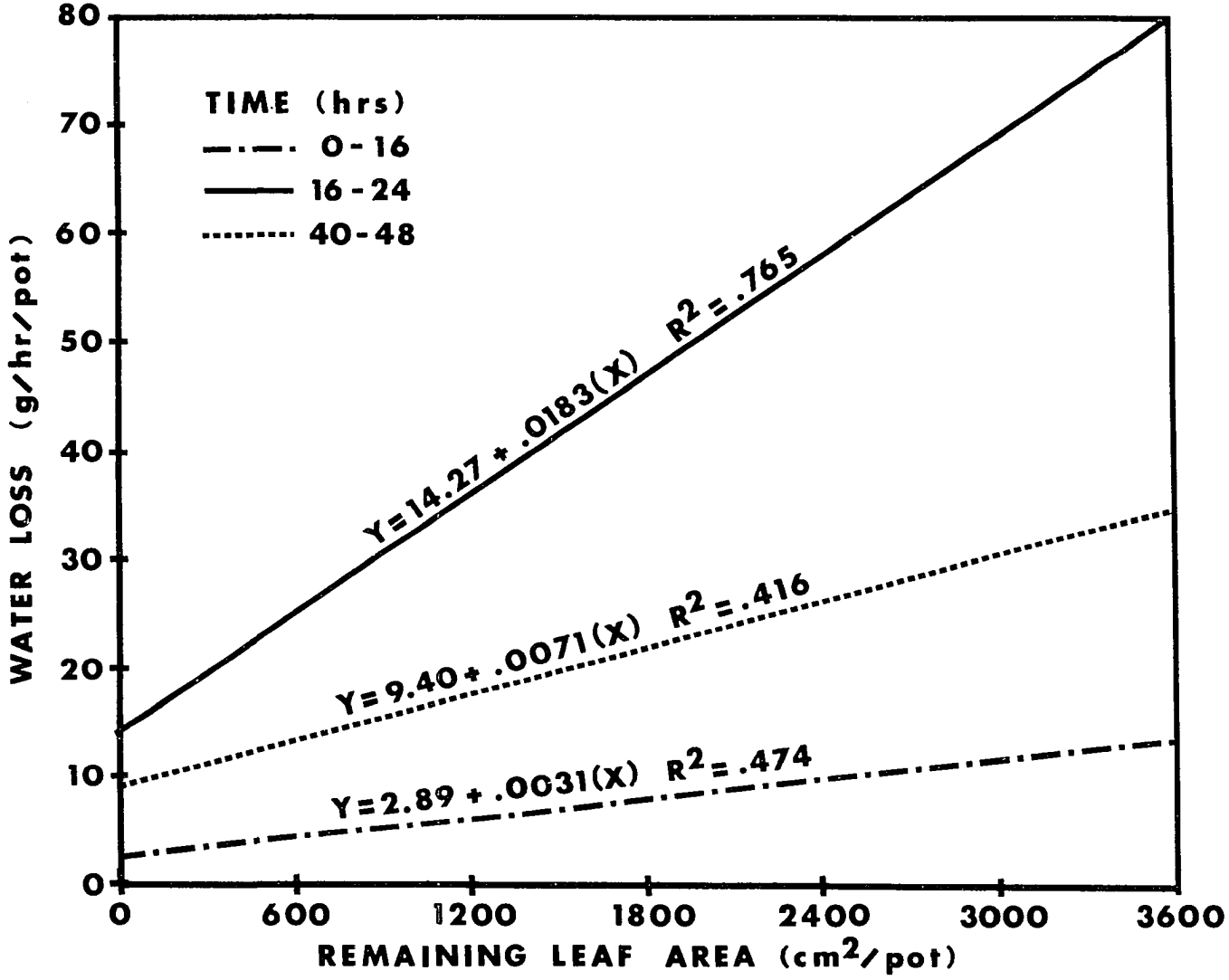

TIME (hrs)
0-16
16-24
40-48
Y=14.27 + .0183(X) R2 = .765
Y=9.40 + .0071(X) R2 = .416
Y=2.89 + .0031(X) R2 = .474
WATER LOSS (g/hr/pot)
REMAINING LEAF AREA (cm2/pot)
0
10
20
30
40
50
60
70
80
0
600
1200
1800
2400
3000
3600

Table 2. Estimates and significance of linear coefficients for leaf area and cut edge from an analysis of covariance for soybean water loss following defoliation

Time period (postdefoliation)	Area			Cut edge[a]		
	Estimate	Pr>|t|[b]	Pr>F[b]	Estimate	Pr>|t|[b]	Pr>F[b]
0-16 hours	.0027650	.0001	.0001	.0025728	.0003	.0001
16-24 hours	.0173806	.0001	.0001	-.0003759	.8808	.6481
40-48 hours	.0073003	.0001	.0001	-.0013742	.5003	.7827

[a]The analysis of covariance which included cut edge did not involve water-loss from pick-defoliated soybean.

[b]See text for description of statistical tests.

coefficient (Pr>|t|) expresses the probability that the regression coefficient is significantly different from zero. The second value (Pr>F) indicates whether the regression variable explains a significant proportion of experimental variability. As expected, leaf area made a significant contribution to water loss during all three periods. Cut leaf edge, however, only made a significant, positive contribution to water loss during the first 16 hours. The transitory importance of cut leaf edge confirmed our earlier conjecture about a healing response.

Least squares means of water loss, adjusted for differences in leaf area between defoliation methods, are presented in Table 3. Defoliation methods produced significant differences in water loss only in the first period. Experimental conditions during this period, e.g., low light environment, saturated soil, and freshly defoliated leaves, were designed to accentuate any treatment differences. Even under conditions favorable for uncontrolled water loss, differences of only 1-2 g/hr/pot were detected. Over the entire experiment, this represented only a 2-5% contribution to total water loss. Consequently, no differences in total water loss were found between defoliation methods.

During the first 16 hours after defoliation, insect-defoliated plants lost water at a higher rate than manually-defoliated plants. Punch and GCW defoliation, however, produced statistically equivalent rates of water loss. Pick defoliation, which removed leaf area with the least tissue damage, produced less water loss than either insect defoliator. With the exception of pick defoliation, differences between methods seemed related to the ratio of cut edge to removed leaf area. This ratio (Table 1) provides

Table 3. Least squares means of hourly and total water loss from soybean plants defoliated by lepidopteran larvae and simulation methods

Defoliation treatment	Hourly water loss (g/hr/pot) Time period (hrs postdefoliation 0-16[a]	16-24[a]	40-48[a]	Total water loss (g/pot)[a]
Green cloverworm	7.54 ab	39.58 a	17.57 a	578.8 a
Cabbage looper	8.25 a	39.71 a	19.88 a	612.3 a
Picking leaflets	6.20 c	37.24 a	18.91 a	564.1 a
Punching holes	6.62 bc	37.67 a	19.62 a	578.3 a

[a]Means followed by different letters are significantly different ($P < 0.05$) by single comparison t-tests. Consequently, the overall protection level may exceed $p = .05$.

an idea of the hole characteristics produced by each defoliation method (Figure 3). For example, CL defoliation, which produced the greatest water loss, created the smallest holes and the largest ratio. Conversely, punch defoliation, which generated the least water loss, produced the largest holes and the smallest ratio. Finally, GCW defoliation, which elicited moderate water loss, left holes intermediate in size and ratio between CL and punch defoliation. Although cut edge may contribute to method differences (Tables 1 and 3), these differences persisted even when cut edge was included as a covariate. Thus, method differences seem related to basic characteristics of the "holes" produced by each defoliation technique. The mechanism behind soybean's transitory response to defoliation method may involve differences in the number and size distribution of leaf veins severed by insect feeding or damage simulation. This finding suggests that closer fidelity of punch defoliation to CL or GCW defoliation may be

achieved by changing punch diameter to approximate the hole characteristics of the insect defoliator. This option is not available with pick defoliation. In view of the transitory effect of defoliation method on water loss, the precaution of adjusting punch size probably is unwarranted.

The differences detected between defoliation methods within the first 16 hours agree with those reported by Hammond and Pedigo (1981); however, these differences were transitory. The overwhelming dominance of remaining leaf area and an apparent "healing" response minimized any differences caused by defoliation methods. In general, soybean response to defoliation, as measured by total water loss, was largely unaffected by the choice of defoliation method. Therefore, both punch and pick simulation methods produced acceptable fidelity in soybean water loss to actual insect defoliation.

PART II. SOYBEAN RESPONSE TO SIMULATED GREEN CLOVERWORM DEFOLIATION: PROGRESS TOWARDS COMPREHENSIVE ECONOMIC INJURY LEVELS

ABSTRACT

Soybean vegetative and yield responses to simulated green cloverworm (GCW) (*Plathypena scabra* [F.]) defoliation were investigated in Iowa from 1980 to 1982. Defoliation levels, ranging from 0 to 180 GCW larval equivalents per m of row, were imposed during full bloom to simulate defoliation by first generation GCW. Defoliation produced linear reductions in leaf area, height, and lodging susceptibility. Compensation through lower leaf retention was transitory and limited. Despite defoliation exceeding 30%, vegetative and reproductive phenology was not disrupted. Simulated GCW defoliation produced significant yield losses, primarily through reduced pod numbers and secondarily through decreased seed weight. The economic injury level for first generation GCW larvae was established at 23 larval equivalents per m of soybean row. In addition, comprehensive economic injury levels, which reflect rainfall variation, were derived.

INTRODUCTION

The economic injury level concept forms the backbone of insect pest management. Stern et al. (1959) outlined the basic definitions of economic damage, economic injury level (EIL), and economic threshold (ET) which underlie the decision-making processes in pest management programs. The EIL concept integrates biology of the crop-pest system and agricultural economics. Consequently, economic injury levels are not developmentally static but evolve through a series of developmental stages as knowledge of the crop, insect pest, and their interaction increases (Poston et al., 1983). These stages include: (1) no economic decision criteria; (2) nominal decision criteria; (3) calculated decision criteria; and (4) comprehensive economic decision criteria. Derivation of economic decision criteria for the green cloverworm (GCW) (*Plathypena scabra* [F.]) on soybean provides an excellent example of these developmental stages.

The GCW is a sporadic pest of soybean in Iowa and throughout the Midwest (Pedigo et al., 1973). A comprehensive hypothesis of GCW population dynamics in Iowa is provided by Buntin and Pedigo (1983) and Pedigo et al. (1983). Two larval generations occur in soybean. The first generation defoliates soybean at the full bloom stage in July, while the second generation damages soybean during the pod- to seed-filling stages in August. Outbreak configurations are typified by a large first generation followed by a smaller second generation. Larval densities during the first generation of an outbreak configuration occasionally exceed economic thresholds (>30 GCW larvae/60 cm of row) (Pedigo et al., 1983). In contrast, larval densities during the second generation of an outbreak configuration fall

well-below the economic threshold for pod- and seed-fill (>24 GCW larvae/60 cm of row) with the onset of an epizootic by *Nomuraea rileyi* (Farlow) (Pedigo et al., 1983). Consequently, the GCW usually poses a threat to Iowa farmers only during full bloom (R2).

Evolution of economic decision criteria for the GCW has proceeded relatively rapidly through the developmental stages described by Poston et al. (1983). Although the green cloverworm was widely recognized as a pest of soybean (Sherman, 1920), no economic decision levels were available to Iowa producers before the 1960s. Establishment of nominal thresholds, 5-10 larvae per 30 cm of row (Stockdale, 1966), coincided with extensive outbreaks of the GCW in the Midwest during 1966 and 1968 (Stone and Pedigo, 1972). These outbreaks also prompted research which established "calculated EILs" for the GCW. Calculated EILs are derived from four primary determinants: control costs, crop market value, injury potential per individual pest, and the damage-loss relationship (Stone and Pedigo, 1972). Combining GCW consumption data with agronomic studies on soybean response to simulated hail defoliation (Kalton et al., 1949), Stone and Pedigo calculated EILs for successive stages of soybean development. Later, refinement of these EILs was deemed necessary because hail simulation methods produced damage distinctly different in appearance, vertical distribution, and phenology from natural GCW defoliation. Therefore, Poston and Pedigo (1976), with further modification by Hammond and Pedigo (1982), developed a hole-punching technique for simulating the appearance, vertical canopy distribution, and phenology of defoliation by first generation GCW larvae. Fidelity of this simulation method to GCW defoliation, in terms of net

photosynthesis and water loss, has been verified (Poston et al., 1976; Hammond and Pedigo, 1981; Part I). Subsequently, this simulation method has been used to refine EILs for first generation GCW larvae (Hammond and Pedigo, 1982; Higgins et al., 1984).

Continuing progress toward the final developmental stage, comprehensive EILs, requires research on how other crop pests and the abiotic environment affect the damage-loss relationship for the pest (Poston et al., 1983). Research on GCW EILs is currently proceeding at this level, as indicated by two recent studies. First, Higgins et al. (1984) explored the interactive effects of GCW defoliation and velvetleaf competition on soybean yield. Additive yield responses in this study suggested that GCW EILs need not reflect the competitive stress of moderate velvetleaf populations. Second, Hammond and Pedigo (1982) documented the effect of drought on GCW economic decision levels, but sufficient data are lacking to incorporate drought effects into comprehensive EILs. Poston et al. (1983) suggest that a basic understanding of how plants respond to insect stress is required before the interactions of biotic and abiotic stressors on crop yield can be fully incorporated into comprehensive EILs.

The objectives of our research on soybean response to simulated GCW defoliation were: (1) to gather basic data on changes in soybean morphology, development, yield, and yield components following defoliation; (2) to refine current calculated EILs for the GCW; and (3) to develop comprehensive EILs for the GCW reflecting rainfall variation.

MATERIALS AND METHODS

Experiments were conducted from 1980-1982 on a Coland clay loam soil (fine-loamy, mixed, mesic Cumulic Haploquoll) near Ames, IA. Soybean was overseeded into 76-cm wide rows on 22 May 1980, 20 May 1981, and 2 June 1982. Within three days after emergence, each row was hand-thinned to a density of 30 plants per m in 1980 and 1981, and 26.7 plants per m in 1982.

Soybean response to defoliation was evaluated using a split-plot design. Main plots specified levels of defoliation and subplots designated the simulation method used to impose this defoliation. The main plots, each measuring 25 m x 5 rows were arranged in a randomized complete block design with four replications in 1980 and 1981 and five replications in 1982. Each year, main-plot treatments simulated GCW defoliation in incremental densities of "larval equivalents." A larval equivalent was defined as the total consumption of one GCW larvae from egg hatch to pupation (54.3 cm^2) (Hammond et al., 1979b). Defoliation levels varied slightly each year, depending on the predefoliation leaf area index (LAI) of the soybean canopy at early bloom (stage R1) (Fehr and Caviness, 1977). Simulated GCW densities, expressed as larval equivalents per m of row, included: 1980 - 0, 60, 120 and 180; 1981 - 0, 80, 120 and 160; and 1982 - 0, 60, 120 and 180. These levels were chosen because they encompassed the full range of reported GCW densities.

Subplots, each three rows x 3 m, were located within each main plot on the basis of stand (30 or 26.7 plants per m) and uniform plant morphology. The number of subplots varied from three in 1980 to six in 1981 and 1982. Subplot treatments designated the combination of defoliation technique (the

way in which leaf material is removed) and temporal pattern of defoliation (the distribution of defoliation over time) used to defoliate the center row of each subplot. During 1980 and 1981, subplot treatments included a factorial combination of two commonly-used defoliation techniques, picking entire leaflets (Todd and Morgan, 1972) and punching holes in leaflets (Hammond and Pedigo, 1982), and three temporal patterns of defoliation, one-day, equal, insect-model. The insect-model temporal pattern was designed to mimic the consumption pattern of GCW larvae. Utilizing a leaf consumption model for the GCW (Hammond et al., 1979b) and a thermal-unit model (Hammond et al., 1979a), Higgins et al. (1983) outlined a procedure which generated realistic rates of defoliation over a 12-day period. One-day defoliation (Todd and Morgan, 1972) was performed when the insect model reached 50% of its projected consumption, typically on the eighth day. Finally, in equal defoliation, the total leaf area to be removed was equally subdivided between each day of the 12-day defoliation period. During 1980, only three subplot treatments were used: (1) punch defoliation following the insect model; (2) pick defoliation following the insect model; and (3) pick defoliation on one day.

Integrity of the defoliation treatments was preserved through several measures. First, to eliminate possible treatment confounding due to handling of plants during defoliation, soybeans in the control plots and one-day defoliation plots were handled each day. However, Thomas et al. (1978) indicate that these measures may not be necessary. Secondly, the outside two rows of each subplot and a 0.5 m buffer at the end of each subplot were sham-defoliated to an equivalent degree as the center row. Finally, to eliminate additional GCW defoliation from naturally-occurring larvae of

generations I and II, each plot was sprayed with a commercial formulation of *Bacillus thuringiensis* Berliner.

A primary objective of our experimental procedures was to produce defoliation simulating the natural damage phenology of the GCW in Iowa soybean. Pedigo et al. (1983) found that damaging GCW populations typically occurred in Iowa soybean during full bloom. Two precautions were taken to insure synchrony of our experimental system with the natural system. First, soybeans were planted at normal planting times for central Iowa. Secondly, local fields were scouted to ascertain GCW phenology. Defoliation was initiated only when mean development of GCW larvae was at or near the third stage and soybeans were in full bloom (R2). When these conditions were met, peak defoliation of our experimental system matched the peak defoliation period of the natural GCW population. Defoliation for equal and insect-model defoliation was initiated on 14 July 1980, 13 July 1981, and 19 July 1982. One-day defoliation was imposed on 21 July 1980, 20 July 1981, and 26 July 1982.

Morphological characteristics and phenological development of soybeans were monitored once before and two to three times after defoliation. Predefoliation measurements were used to evaluate the uniformity of plots and provide estimates of LAI for determining desired defoliation levels. No differences in predefoliation measurements were detected between treatments. Postdefoliation measurements were designed to examine the soybean's morphological and phenological responses to defoliation. Data on plant height, vegetative and reproductive stages (Fehr and Caviness, 1977), trifoliolate number, lowest leaf-bearing node, and branching were recorded from three plants per subplot. Leaf area was measured on each plant using

a LiCor® LI-3000 portable leaf area meter. All measurements were made nondestructively.

Preharvest lodging was evaluated in all plots during 1980 and 1982. Lodging of each subplot was rated on a 1-5 scale with 1 designating an upright plant (90° from horizontal) and 5 designating a completely lodged plant (0° from horizontal). No data were gathered on lodging in 1981 because a severe storm simultaneously lodged all plots.

Before harvest, final stand counts and lodging ratings were made on each subplot. Harvest took place in two steps. First, a subsample of plants was selected from each plot for determination of yield components: 6 plants/plot in 1980; 9 plants/plot in 1981; and 15 plants/plot in 1982. Each plant was selected on stratified random basis. Positions within each plot were selected at random and the five-plant grouping nearest the position was examined. The median plant, in stem-base diameter, was selected for the yield component subsample. Atypical plants, such as Y-plants, runts, and diseased plants, were not selected for yield component subsamples. Data collected from this subsample included total plant weight, seed weight, apparent harvest ratio, pods per plant, seeds per plant, seeds per pod, and seed size (seed hundredweight). The second step in the harvest sequence included cutting the remaining plants in each subplot and double-threshing each sample. Data recorded on each yield sample included total above-ground plant weight and seed weight. Subsample totals were added to sample totals and seed weight adjusted to 13% moisture before the statistical analyses.

Data on all variables were analyzed using standard ANOVA techniques for a split-plot design. Significant differences because of defoliation level, defoliation method or their interaction were isolated using orthogonal treatment comparisons. This paper presents the results of the main-plot experiment, the effects of defoliation level on soybean morphology, development, and yield components. Part III will explore the effects of simulation method on soybean response to defoliation.

RESULTS AND DISCUSSION

Soybean Morphology and Development

Simulated GCW defoliation produced distinct changes in plant morphology each year. Variables, besides leaf area, which were affected by defoliation included height, trifoliolates per plant, and lowest leaf-bearing node (Table 1). In contrast, defoliation did not produce detectable changes in soybean development. Despite defoliation exceeding 25-30%, synchrony of reproductive development and the development of mainstem nodes was not disrupted. No differences in total nodes per plant (mainstem nodes plus branch nodes) or branches per plant were detected in any year.

Defoliation treatments reduced leaf area per plant and LAI from 0 to ca. 30% (Table 2). In each year, leaf area per plant and LAI declined more than was predicted by the imposed defoliation level. Leaf area reductions for each defoliation level are translated into larval equivalents in Table 2. Realized larval equivalents exceeded imposed larval equivalents from 10 to 70%. Two reasons for this discrepancy seem plausible. First, based on the vertical distribution of GCW larvae (Pedigo et al., 1973), defoliation was imposed on the upper 1/3 to 1/2 of the soybean canopy. This portion of the canopy contains expanding leaves on which GCW larvae readily feed. Removal of expanding leaf tissue has a greater effect on remaining leaf area than removal of mature, fully-expanded leaf tissue. For example, removal of 10 cm^2 from a 50% expanded leaf would translate into ca. 20 cm^2 of the same leaf when fully expanded (assuming no effects on leaf expansion). Secondly, partial defoliation of an expanding leaf may affect its ability to complete expansion. This finding emphasizes the importance of mimicking

Table 1. Effects of simulated green cloverworm defoliation on soybean leaf area, trifoliolate number, lowest leaf-bearing node, height and lodging score

Variable	1980					1981	
	Date[a]	A[b]	B[b]	p[c]	R^{2d}	Date[a]	A[b]
Leaf area (cm^2/plant)	2	1424	-8.56	<.001	.811	5	1132
	12	1448	-7.74	<.001	.881	19	1345
	18	1444	-7.76	<.001	.837		
Trifoliolate number						5	8.87
						19	11.28
Lowest leaf-bearing node	2	3.98	-.007	.003	.324	5	4.80
	18	4.72	-.011	<.001	.465	19	5.24
Height (cm)	2	117.3	-.093	.016	.174	5	92.4
	12	118.9	-.079	.028	.119	19	103.6
	18	119.0	-.055	.123	.074		
Lodging score	25	3.20	-.011	.063	.192		

[a]Days postdefoliation.

[b]Intercept (A) and regression coefficient (B) from the linear regression $y = A+Bx$, where x = no. GCW larval equivalents/30 cm of row.

[c]Significance of linear regression based on F-value with 1 and 9 df in 1980-1981, and 1 and 12 df in 1982.

[d]Proportion of main plot variability explained by linear regression.

[e]Where regressions were not significant, only the mean across all defoliation levels is presented.

1981					1982		
B[b]	p[c]	R^2[d]	Date[a]	A[b]	B[b]	p[c]	R^2[d]
-7.55	<.001	.764	5	1475	-7.37	<.001	.580
-7.02	<.001	.729	31	1508	-8.15	<.001	.785
.0094	.077	.167	12	11.38	---	n.s.[e]	---
.0168	.006	.429					
---	n.s.[e]	---	12	5.16	-.006	.174	.119
-.012	.046	.322					
---	n.s.[e]	---	12	127.9	-.151	.001	.221
---	n.s.[e]	---					
			4	2.24	-.023	<.001	.694

Table 2. Leaf area indices (LAI), realized defoliation level, and yield of soybean following simulated GCW defoliation

Defoliation[b] level	LAI[a]			Realized defoliation	
	1980	1981	1982	1980	1981
0	5.23 (0)[c]	4.84 (0)	5.10 (0)	0	0
18	4.53 (13.4)		4.52 (11.8)	30.6	
24		4.17 (13.9)			28.2
36	3.90 (25.5)	3.80 (21.7)	4.15 (18.6)	58.2	43.6
48		3.48 (28.4)			57.2
54	3.61 (31.1)		3.62 (29.0)	71.0	

[a]Average of postdefoliation measurements.

[b]Expressed as GCW larval equivalents/30 cm of row.

[c]Numbers in parentheses indicate percent reduction from the undefoliated check.

Level[b]	Yield (g/3.0 m)		
1982	1980	1981	1982
0	822.4 (0)	908.6 (0)	886.6 (0)
24.7	831.5 (1.11)		834.8 (5.84)
		873.2 (3.90)	
39.9	775.0 (5.76)	849.4 (6.52)	819.0 (7.62)
		807.5 (11.13)	
62.2	750.4 (8.75)		737.6 (16.81)

the vertical distribution of insect damage within the plant (Hinson et al., 1978).

Defoliation treatments produced linear reductions in leaf area per plant and LAI immediately following defoliation. For simplicity, only the linear regressions for leaf area per plant are presented (Table 1). Linear relationships persisted through the remainder of the growing season in all years. During 1980 and 1982, leaf area per plant and LAI were relatively stable following defoliation, as evidenced by the small changes in intercepts. This stability indicated that leaf area lost through abscission of lower nodes was approximately equal to leaf area gained through leaf expansion and addition of new leaves. In 1981, soybeans compensated for development retarded by drought through the rapid addition of new leaves and increased leaf expansion when normal rains resumed. During 1980 and 1981, slopes tended to decrease with time after defoliation, suggesting a slight compensatory response. In all years, however, the differences in slope were not significant. Thus, compensation was minimal.

Compensatory response of soybeans to defoliation could take two forms; either lower leaves can be retained, or the expression and expansion of upper leaves can be accelerated (Higgins et al., 1983). Linear relationships between defoliation level and lowest leaf-bearing node clearly demonstrated that leaf retention occurred in 1980 and 1981 (Table 1). A similar, though insignificant, trend developed in 1982. Higgins et al. (1983) reported the same pattern of lower leaf retention following simulated GCW defoliation. Further evidence of lower leaf retention was provided by leaf area measurements. Analysis of leaf area, by stratum, indicated that defoliated plants

possessed greater leaf area in the lower abscission stratum during 1980 and 1981 (Part IV). In contrast to developments within the lower stratum, little evidence of compensation was found within the upper undefoliated stratum. No differences in leaf area were detected within this stratum in any year (Part IV). The only evidence of compensation in this upper strata of leaf development and expansion was found in 1981. During 1981, when significant postdefoliation growth occurred, defoliated plants possessed slightly more trifoliolates (Table 1). This increase in trifoliolate number reflected both lower-leaf retention and accelerated development of upper leaves. Defoliated plants exhibited a trend, though insignificant, for more mainstem nodes. These findings collectively demonstrate that soybean compensation may take both forms; however, lower-leaf retention contributed the majority of leaf area. Leaf area compensation of soybean to simulated GCW defoliation, although clearly evident, was not expected to produce detectable yield compensation for two reasons. First, the response was extremely limited, replacing less than 17% of the leaf area removed by defoliation. Secondly, because indeterminate soybeans were switching from vegetative to reproductive growth, compensation was limited principally to lower-leaf retention. This retention was transitory, and, given the reduced photosynthetic capacity of lower leaves, it is doubtful that delayed abscission translated into yield compensation. This finding agrees with Boote's (1981) contention that the widely accepted concept of "compensatory regrowth" following defoliation is largely a myth.

Linear reductions in height with increasing defoliation levels occurred in 1980 and 1982 (Table 1). Similar trends, though insignificant,

were observed in 1981. Rapid growth in 1981 following defoliation presumably masked this trend. Height reductions following defoliation are widely reported for indeterminate soybeans (Kalton et al., 1949; Hammond and Pedigo, 1982), but no mechanism has been proposed for these height reductions. Because no differences in development of mainstem nodes was detected, height reductions reflected a shortening of internodes. Several factors may contribute to this response including reduced photosynthate availability, moisture stress, and reduced lodging susceptibility. During 1980, a year of moderate drought, defoliation seemingly enhanced water stress sufficiently to retard internode elongation. With the resumption of rainfall in early August, this effect diminished (Table 1). In 1982, a different factor, lodging, seemingly contributed to the height differential. Lodged plants tended to elongate in the upper nodes through phototropic growth movements. Consequently, defoliated plants, which were less susceptible to lodging, underwent less internode elongation.

Lodging scores differed between defoliation levels in 1980 and 1982. In both years, lodging severity decreased with increasing defoliation level. Kalton et al. (1949), Fehr et al. (1977), and Higgins et al. (1983) reported similar reductions in lodging susceptibility. Lodging typically occurs in Iowa soybean fields following late-season thunderstorms with gusty winds. Reduction in lodging is attributed to both the direct effect of reduced leaf area and the indirect effect of decreased plant height. Defoliated plants with reduced leaf area and stature presumably presented a smaller effective surface for the wind's force. Gradually, as the season progressed, even the defoliated plots lodged. At harvest, no differences in lodging score were detected in any year. Similar differences were noted

in 1981, but a severe store eliminated the pattern before lodging scores were taken. Higgins et al. (1983) reported a similar reduction in lodging susceptibility following defoliation and suggested that lodging might be an integral component of the yield-loss relationship. Lodging is known to reduce yield of undefoliated soybean (Johnston and Pendleton, 1968). Delayed onset and reduced severity of lodging following defoliation imply that lodging effects on yield will be reduced by defoliation. Consequently, decreased lodging susceptibility may partially offset the potential yield reductions caused by defoliation (Higgins et al., 1983). The magnitude of this interaction will depend on the timing and severity of both defoliation and lodging.

Yield and Yield Components

Simulated GCW defoliation significantly reduced yield and yield components each year (Tables 2 and 3). Traditionally, entomologists searching for damage-loss relationships treated the plant as a "black box" by focusing solely on yield, a seasonal endpoint. The trend towards comprehensive economic levels (Poston et al., 1983), however, requires a greater understanding of how the plant responds to pest stress and how this stress translates into yield reductions. Analyses of yield components provide a valuable tool for understanding how insect-imposed stress translates into yield loss.

Final yield is related to the soybean's accumulation of photosynthetic energy and the way in which this energy is divided between structural and reproductive components. This relationship is expressed in the following equation:

Table 3. Response of soybean yield and yield components to simulated green cloverworm defoliation

Variable	1980				1981
	A[a]	B[a]	p[b]	R^2[c]	A[a]
Plot					
Total weight (g/3.0m)	1575	-2.64	.040	.218	1856
Seed weight (g/3.0m)	836	-1.60	.027	.275	914
Harvest ratio	.5032	---	n.s.	---	.4956
Subsample[d]					
Total weight (g/3.0m)	25.83	-.062	.001	.345	25.84
Seed weight (g/3.0m)	15.40	-.044	.001	.452	15.90
Harvest ratio	.5695	-.00030	.014	.207	.5902
Pod number/plant	27.88	-.066	.007	.239	27.77
Seed number/plant	71.67	-.162	.009	.239	66.11
Seeds per pod	2.581	---	n.s.	---	2.407
Seed weight (g/100 seeds)	21.55	-.015	.183	.118	23.05

[a]Intercept (A) and regression coefficient (B) from the linear regression $y = A+Bx$, where x = no. GCW larval equivalents/30 cm of row.

[b]Significance of linear regression based on F value with 1 and 9 df in 1980-1981 or 1 and 12 df in 1982.

[c]Proportion of main plot variability explained by linear regression

[d]Subsamples included 6 (1980), 9 (1981), and 15 (1982) plants. Selection procedures produced a positive bias by eliminating runts, Y-plants, and diseased. Consequently, subsample relationships, if extrapolated to the whole plot, overestimate defoliation effects on the plot.

1981			1982			
B[a]	p[b]	R^2[c]	A[a]	B[a]	p[b]	R^2[c]
-4.97	.003	.437	1683	-4.43	.004	.377
-2.02	.005	.343	890	-2.60	.004	.401
---	n.s.	---	.5232	---	n.s.	---
-.084	.001	.413	24.57	-.084	.001	.364
-.050	.001	.378	14.03	-.052	.001	.338
---	n.s.	---	.5718	-.00022	.093	.067
-.065	.005	.185	29.20	-.087	.001	.301
-.134	.017	.149	72.34	-.217	.001	.272
---	n.s.	---	2.475	---	n.s.	---
-.028	.001	.209	19.45	-.017	.002	.153

Yield/plant = Total Plant Weight * Apparent Harvest Ratio (1).

Apparent harvest ratio (seed weight/total above-ground plant weight) provides an index of how total photosynthate is partitioned between structural and reproductive components.

Yield also may be expressed as the product of several yield components which are successively determined as the growing season progresses. This relationship is expressed in the following model:

Yield/Plant = Nodes/Plant * Pods/Node * Seeds/Pod * Weight/Seed (2).

The impacts of simulated GCW defoliation on soybean and its response to this stress are reflected in these yield components (Table 3).

Simulated GCW defoliation produced linear reductions in yield and above-ground dry weight in all years (Table 3). Apparent harvest ratio was relatively unchanged on a plot basis. Analyses of apparent harvest ratio from 6 and 15 plant subsamples gave significant but slight linear reductions following simulated GCW defoliation in 1980 and 1982. No difference in apparent harvest ratio was detected from 9 plant subsamples in 1981. Regression analyses combining years indicated the overall relationship between harvest ratio and defoliation level was insignificant. Therefore, yield reductions were proportional to the reduction in total plant weight. Soybean compensation to defoliation, through increased partitioning of energy to reproductive components, was not found.

Simulated GCW defoliation affected yield components differentially (Table 3). The greatest impact occurred on the number of pods per plant. Defoliation levels greater than or equal to 160 GCW larval equivalents per m reduced pod number by 12.0%, 11.2%, and 17.1% in 1980 to 1982,

respectively. As discussed previously, defoliation at stage R2 to R3 did not alter vegetative development. Consequently, the number of nodes per plant was similar, regardless of defoliation level. Defoliation produced linear reductions in pod number per plant in all three years. Considering the constancy of nodes per plant, it may be inferred that defoliation reduced pods per node. Reduced pod number could indicate reduced ability to set pods or increased pod abortion even if pods are set. Similar reductions in pod number have been reported following simulated insect defoliation at stages R2 to R3 (Thomas et al., 1976; Hammond and Pedigo, 1982; Higgins et al., 1984).

The number of seeds set per pod varied significantly between years with 2.58, 2.41, and 2.47 seeds per pod in 1980 to 1982, respectively. Defoliation had no apparent effect on seed set because significant differences in the number of seeds per pod were not detected. Consequently, reductions in seed number per plant with defoliation level were proportional to the reduction observed in pod number (Table 3). Reductions in seed number per plant following defoliation at stages R2 to R3 are commonly reported (Fehr et al., 1977; Hammond and Pedigo, 1982; Higgins et al., 1984).

Simulated GCW defoliation also produced significant linear reductions in seed size in 1981 and 1982. A similar, though insignificant, trend was observed in 1980. Defoliation exceeding 160 GCW larval equivalents per m of row reduced seed size 2.8%, 6.0%, and 4.1% in 1980 to 1982, respectively. Reductions in seed size also have been reported in other studies (Kalton et al., 1949; Todd and Morgan, 1972; Hammond and Pedigo, 1982). In this study, reduction was considerably less than the reduction in pods per plant. Thus, yield reductions primarily reflected reduction in pod number

and secondarily decreased seed size.

Seed size, like seeds per pod, varied significantly between years. Average seed size was 21.16, 22.23, and 19.02 g/100 seeds for 1980 to 1982, respectively. Seed size is known to be a function of photosynthetic source to sink ratio. Consequently, differences in seed size between years could represent differences in this ratio. To investigate this hypothesis, a regression analysis was performed relating seed size to source size per seed (cm^2 of leaf area per seed). Within each year, reduced seed size was linearly related to reduced source size per seed. Differences between years were significant, suggesting that an external factor differentially influenced source capacity between years. Differences between years may be related to lodging patterns, precipitation, or an interaction of these factors. The importance of precipitation is suggested by a strong correlation ($r = 0.998$, $n = 3$, $p < 0.01$) between seed size and cumulative rainfall during the first 25 days after defoliation.

Determination of Economic Thresholds

Yields declined linearly with defoliation level in all years (Table 3). Thus, soybean displays a "susceptive" response (Poston et al., 1983) to simulated GCW defoliation and, presumably, to actual GCW defoliation. Yield losses, estimated from the slopes of these regression equations, averaged -0.151, -0.202, and -0.260 g per larval equivalent for 1980 to 1982, respectively. A combined regression over all years produced a loss of -0.207 g per larval equivalent. These loss estimates closely agree with estimates by Higgins et al. (1984), who found losses of -0.200 (1980), -0.230 (1981), and -0.222 (combined) g per larval equivalent. In contrast,

Hammond and Pedigo (1982) found an average loss of -0.46 g per larval equivalent. All of these studies on soybean response to simulated GCW defoliation were conducted in the same locale using the same experimental methods and soybean variety. Consequently, differences in loss estimates between these studies seem related to environmental variability between years.

Soil moisture conditions varied substantially between years. Total seasonal rainfall (May to September) and subtotals, reflecting rainfall before, during, and after defoliation, are presented in Table 4. Because moisture stress involves the integration of several factors besides precipitation, a moisture-stress index (Shaw's (1974) raw index) also is presented in Table 4. Moderate to severe drought characterized the 1976 and 1977 growing seasons (Hammond and Pedigo, 1982). During 1976, subnormal rainfall throughout the growing season produced seasonal deficits of 26.2 cm. Although 1977 ended with a seasonal surplus of 8.8 cm, most of the growing season was marked by severe moisture stress (cumulative stress index = 32.7) which persisted well into August. In both 1976 and 1977, canopy development and yield potential were drastically reduced by moisture stress. Hammond and Pedigo (1982) found that these conditions accentuated the yield loss per GCW larval equivalent (-0.46 g per larval equivalent). In contrast, under mild drought to normal moisture conditions (1980 to 1982), both Higgins et al. (1984) and the present study found a lower yield-loss per larval equivalent (ca. -0.21 g). Thus, discrepancies in yield-loss estimates seem related primarily to the timing and severity of moisture stress.

Table 4. Seasonal totals and distribution of precipitation and moisture stress relative to defoliation[a]

Seasonal period	Precipitation (cm)					Moisture stress index[b]				
	1976	1977	1980	1981	1982	1976	1977	1980	1981	1982
Predefoliation	22.1 (-9.0)[c]	11.5 (-17.4)	20.7 (-9.0)	15.7 (-13.7)	37.5 (+6.4)	.45	.44	.08	2.80	0.00
Defoliation	2.5 (-0.8)	2.4 (-0.7)	1.5 (-1.9)	0.2 (-3.2)	0.3 (-3.1)	2.23	2.54	1.72	4.74	0.00
Postdefoliation	1.5 (-16.3)	47.2 (+26.8)	17.8 (-1.5)	27.9 (+8.4)	13.6 (-4.2)	11.89	29.68	7.09	.03	0.07
Total	26.1 (-26.2)	61.1 (+8.8)	40.0 (-12.3)	43.8 (-8.5)	51.4 (-.9)	14.57	32.66	8.89	7.57	0.07

[a]Values based on data from N.O.A.A. station (Index 0200) near Ames, Iowa.

[b]Moisture stress is calculated from the index: stress/day = 1-(ET/PET), where ET = crop evapotranspiration and PET = potential evapotranspiration. This index ranges from 0 to 1 and is accumulated over each period (see Shaw, 1974, for details).

[c]Departure from normal rainfall.

EILs were calculated for first generation GCW larvae using procedures developed by Hammond and Pedigo (1982). Two equations were used in these calculations:

$$\text{Gain Threshold (kg/ha)} = \frac{\text{Management Costs (\$/ha)}}{\text{Soybean Market Value (\$/kg)}} \qquad (3)$$

$$\text{EIL (insects/ha)} = \frac{\text{Gain Threshold (kg/ha)}}{\text{Loss per Insect (kg/insect)}} \; . \qquad (4)$$

Based on current management costs in Iowa ($16.68/ha for aerial application of carbaryl at 1.12 kg a.i./ha) and a soybean market price of $0.27/kg, a gain threshold of 61.8 kg/ha must be exceeded for GCW control to be justified economically. Using our estimates of yield-loss per insect, EILs were established at 409,125 (1980), 305,830 (1981), 237,610 (1982), and 298,445 (combined years) GCW larval equivalents per ha. In 76-cm row widths, these EILs translate to 31, 23, 18, and 23 GCW larval equivalents per m of soybean row, respectivley.

The EILs calculated in this study are comparable to those reported by Higgins et al. (1984), if their EILs are adjusted using a current gain threshold. Noting similarities in seasonal moisture conditions, these loss estimates per insect can be combined to produce an EIL appropriate in near-normal to slightly droughty conditions. Using an average yield-loss estimate from both studies (-0.209 g per larval equivalent), an average EIL of 22.5 GCW per m was calculated for first generation GCW larvae. Hammond and Pedigo (1982) calculated an EIL, adjusted to reflect a current gain threshold, of 10 GCW per m. These authors suggested that use of their EIL be restricted to drought conditions.

The pattern and amount of precipitation during a growing season clearly affect soybean canopy development and, ultimately, soybean response to a given defoliation level. Economic injury levels and thresholds for the GCW should reflect this variability in canopy development. Therefore, we rcommend a system of two EILs for the GCW, a system which should promote more efficient use of farm management resources. Switching to a lower EIL (10 GCW per m of row) during droughts, when canopy development is seriously impaired, should prevent unnecessary yield losses. Conversely, utilizing a higher EIL (22.5 GCW per m of row) under normal to above-normal conditions, should prevent unnecessary insecticide applications. The use of EILs, which incorporate an abiotic factor, such as precipitation, represents progress towards comprehensive decision levels for the GCW in Iowa.

PART III. A COMPARISON OF METHODS SIMULATING INSECT DEFOLIATION OF SOYBEAN

ABSTRACT

Methods simulating insect defoliation of soybean are widely used to develop damage-loss relationships. The objective of this research was to determine if defoliation by several simulation methods elicited equivalent vegetative and reproductive responses. A split-plot design was used to investigate soybean response to simulated green cloverworm (GCW) (*Plathypena scabra* [F.]) defoliation at stage R2. Main plots specified defoliation levels, ranging from 0 to 120 GCW larval equivalents per m of row, and subplot treatments designated the simulation method. Simulation methods included factorial combinations of two defoliation techniques (punching holes in leaflets, picking entire leaflets) and three temporal patterns of defoliation (one-day, equal, insect-model). Both defoliation technique and temporal pattern affected remaining leaf area, height, and yield. Punch-defoliated plants possessed less remaining leaf area, shorter height, and less yield than pick defoliated plants. One-day defoliation resulted in more leaf area, taller plants, and greater yields than either equal or insect-model defoliation. Yield reductions primarily reflected the effects of temporal pattern on pod and seed number and the effects of technique on seed size. Punch-defoliation produced smaller seed size than pick-defoliation because punch-defoliated plants possessed less source size (cm^2 of remaining leaf area) per seed. Simulation methods did not affect the capacity of remaining leaf tissue (g/cm^2). Yield differentials between simulation methods were sufficient to significantly affect yield-loss estimates and economic injury levels (EILs). The most commonly used simulation method, pick defoliation on one day, produced the least yield reductions

and highest EILs. In contrast, punch defoliation following the equal temporal pattern generated the greatest yield reductions and lowest EILs. The remaining four simulation methods elicited similar yield reductions and produced equivalent EILs.

INTRODUCTION

Researching the relationship between insect damage and crop yield-loss is a fundamental necessity for any pest management program. Estimates of yield-loss per insect form one of the four principal factors in calculating economic injury levels (Poston et al., 1983). Conventional methods of obtaining these yield-loss estimates include observing or manipulating natural insect populations, creating artificial infestations, or simulating insect damage. None of these methods offers a panacea because each method possesses its own distinct set of advantages and disadvantages. For example, when working with insect populations (natural or artificial), damage levels are hard to control. Even when damage levels are quantified, relating these levels to a specific insect density can be difficult because of natural mortality or establishment problems. Furthermore, cages designed to contain insects within plots or to exclude natural mortality agents may alter plant response to insect damage. Hammond and Pedigo (1982) and Higgins et al. (1984) discuss the difficulties of working with insect populations in more detail.

A widely used alternative to manipulating insect populations involves the use of various types of damage simulation. With simulation methods, the damage level, distribution of damage within the plant, and the timing of the damage can be precisely imposed. Moreover, damage levels can be easily replicated with simulation methods. Considering the problems which arise when working with insect populations, simulation methods often provide the only reliable and economically-feasible means of determining the damage-loss relationship. Consequently, damage simulation is commonly used

to derive yield-loss relationships. For example, ca. 90% of currently published studies on soybean response to defoliation involved damage simulation. Defoliation produced by simulation methods often differs from actual insect defoliation in its physical appearance, distribution within the soybean canopy, and distribution through time (Ruesink and Kogan, 1975). Although damage simulation provides a valuable tool for approximating the damage-loss relationship, the validity of the damage-loss relationship depends upon the fidelity between the crop's response to simulated and actual insect damage (Poston et al., 1983).

Insect defoliation of soybean has been simulated by a variety of damage methods. Throughout this paper, the term "simulation method" will be used to desribe specific combinations of defoliation technique (the way in which leaf area is removed), temporal pattern of defoliation (the distribution of defoliation through time), and damage distribution within the plant. Commonly used defoliation techniques include: (1) punching holes in leaflets (Higgins et al., 1983; Hammond and Pedigo, 1982); (2) picking entire leaflets (Todd and Morgan, 1972; Thomas et al., 1974); (3) cutting terminal portions of leaflets (Caviness and Thomas, 1980); and (4) combinations of picking entire leaflets and cutting off portions of leaflets (Turnipseed, 1972). Temporal pattern, possibly an important component of damage simulation, has largely been ignored. Consequently, a majority of studies have utilized one-day defoliation -- a phenomenon typical of few insect-pest situations. Several recent studies, however, have duplicated the normal phenology of insect damage (Poston and Pedigo, 1976; Hammond and Pedigo, 1982; Higgins et al., 1983). Similarly, the distribution of defoliation within the plant canopy has been simplified in most damage

simulation studies. Often, the damage is imposed uniformly throughout the soybean canopy. More rarely, the damage is restricted to a certain stratum, which typically contains the damaging stages (Poston and Pedigo, 1976; Hammond and Pedigo, 1982; Higgins et al., 1984). Thus, a wide range of simulation methods are used, which vary in their emphasis on realism in defoliation technique, temporal pattern, and damage distribution within the plant.

Traditionally, use of simulation methods has been based on the assumption that only the quantity of leaf area removed is important and that soybean response to defoliation does not vary between simulation methods. This assumption has been investigated for basic physiological processes, such as photosynthesis and transpiration. Poston et al. (1976) found that simulation methods produced differential effects on photosynthesis of remaining leaf tissue. Defoliation techniques in which the midrib was cut stimulated photosynthesis. In contrast, punching holes and cutting leaflets along the midrib adequately simulated actual insect defoliation. Hammond and Pedigo (1981), measuring water loss from excised soybean leaves, found that punching holes simulated insect defoliation more closely than picking entire leaflets. However, when considering the entire canopy response, both picking leaflets and punching holes in leaflets adequately simulated the effects of two lepidopteran defoliators on water loss (Part III). The assumption that different simulation methods produce equivalent soybean response to defoliation has not been investigated for soybean growth, development, or yield. Moreover, the relative importance of defoliation technique and the temporal pattern of defoliation has not been investigated.

Therefore, this paper evaluates the effects of simulation method on soybean response to defoliation. The objectives of this study were to: (1) compare and contrast the effects of simulation methods on soybean morphology, development, and yield components following simulated insect defoliation; (2) evaluate the relative importance of two aspects of a simulation method, namely, defoliation technique and temporal pattern, to the soybean response; (3) ascertain whether any detectable differences between simulation methods sufficiently affect yield-loss relationships to warrant further validation studies with actual insect defoliation; and (4) provide a data base by which simulation methods can be calibrated against each other if alterations of yield-loss relationships are detected.

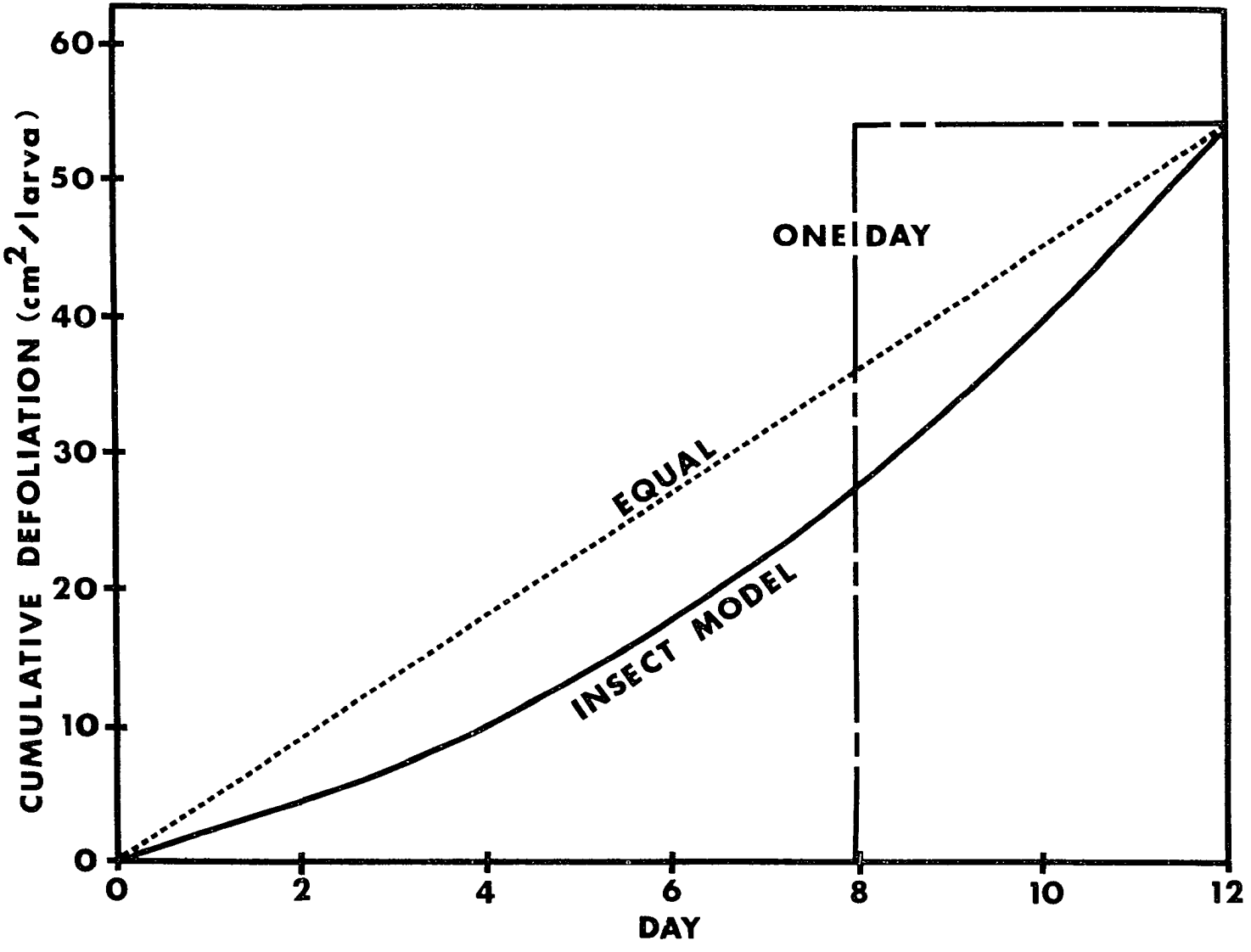
MATERIALS AND METHODS

Soybean response to defoliation by various simulation methods was investigated near Ames, Iowa, during 1980, 1981, and 1982. Soybeans were planted on 22 May 1980, 20 May 1981, and 2 June 1982, in 76-cm wide rows and then hand-thinned to a density of 30 plants per m in 1980 and 1981 and 26.7 plants per m in 1982.

The relative effects of simulation method on soybean morphology, development, and yield components were evaluated using a split-plot design. Main plots specified levels of defoliation and subplots designated the simulation method used to impose this defoliation. This design was chosen to permit maximum delineation of differences between simulation methods. The main plots, each measuring 25 m x 5 rows, were arranged in a randomized complete block design with four replications in 1980 and 1981, and five replications in 1982. Each year, main plot treatments simulated GCW defoliation in increments of "larval equivalents." A larval equivalent was defined as the total leaf consumption of one GCW larvae from egg hatch to pupation (54.3 cm^2) (Hammond et al., 1979b). Defoliation levels varied slightly between years, depending on canopy development. These defoliation levels, expressed in GCW larval equivalents per m of row, were: 1980 - 0, 60, 120, and 180; 1981 - 0, 80, 120, and 160; and 1982 - 0, 60, 120, and 180.

Subplots, each 3 rows x 3 m, were located within each plot on the basis of stand (30 or 26.7 plants per m of row) and uniform plant morphology. The number of subplots varied from three in 1980 to six in 1981 and 1982. Subplot treatments designated the combination of defoliation

Figure 1. Cumulative defoliation (cm^2/larval equivalent) over the 12-day defoliation period for three temporal patterns: insect-model, equal, and one-day


CUMULATIVE DEFOLIATION (cm²/larva)
60
50
40
30
20
10
0
0
2
4
6
8
10
12
DAY
ONE DAY
EQUAL
INSECT MODEL

technique (the way in which leaf area is removed) and temporal pattern of defoliation (the distribution of defoliation through time) used to defoliate the center row of each subplot. During 1981 and 1982, subplot treatments included a factorial combination of two commonly used techniques, picking entire leaflets (Todd and Morgan, 1972) and punching holes in leaflets (Hammond and Pedigo, 1982), and three temporal patterns, insect-model, equal, and one-day. Cumulative defoliation for each of these temporal patterns is depicted in Figure 1. The insect-model temporal pattern was designed to mimic the consumption of GCW larvae. Utilizing a leaf consumption model for the GCW driven by thermal-unit accumulations (base temperature = 52°F) (Hammond et al., 1979a), Higgins et al. (1983) outlined a procedure which generated realistic rates of defoliation over a 12-day period. One-day defoliation (Todd and Morgan, 1972) was performed when the insect model reached 50% of its projected consumption, typically on day 8 of the defoliation period. Finally, in the equal temporal pattern, total leaf area to be removed was equally subdivided between each day of the 12-day defoliation period. During 1980, only three subplot treatments were used: (1) punch defoliation following the insect model; (2) pick defoliation following the insect model; and (3) pick defoliation on one day.

Integrity of defoliation treatments was preserved through several measures, which are extensively discussed by Hammond and Pedigo (1982) and Higgins et al. (1983). Basically, these measures were designed to eliminate treatment confounding caused by handling the soybean leaves, competition from neighboring undefoliated plants, and additional defoliation from natural GCW populations. Several precautions also were taken to insure

synchrony between our experimental system and the natural GCW-soybean system. Pedigo et al. (1983) found that damaging GCW outbreaks typically occur in Iowa soybean during the full bloom stage. Therefore, defoliation treatments were initiated only when mean development of field GCW larvae was at the third stage and soybeans were in full bloom (R2). These conditions were met and defoliation initiated on 14 July 1980, 13 July 1981, and 19 July 1982. One-day defoliation occurred on 21 July 1980, 20 July 1981, and 26 July 1982.

Morphological characteristics and phenological development of soybeans were monitored two or three times after defoliation. Measurements were taken immediately after defoliation to assess the direct defoliation effects and then two to four weeks later to monitor the indirect defoliation effects. Data on plant height, vegetative and reproductive stages (Fehr and Caviness, 1977), trifoliolate number, lowest leaf-bearing node, and branching were recorded from three plants per subplot on each sampling date. Leaf area also was measured nondestructively using a LiCor® LI-3000 portable leaf area meter. Preharvest lodging was rated on a 1-5 scale, with 1 designating an upright plant (90° from horizontal) and 5 designating a completely lodged plant (0° from horizontal). Final stand counts and lodging ratings also were taken on the plots before harvest.

Harvest was performed in two steps. First, a subsample of plants were selected from each plot for determination of yield components: 6 plants/plot in 1980; 9 plants/plot in 1981; and 15 plants/plot in 1982. Each plant was selected with a stratified random procedure. Positions within each plot were chosen at random. The median plant, in stem-base

diameter, of the five-plant grouping nearest the position was selected for the yield component subsample. Atypical plants, such as Y-plants, runts, and diseased plants were avoided. Data collected from this subsample included: total plant and seed weight, apparent harvest ratio, pods per plant, seeds per plant, seeds per pod, and seed size (seed hundredweight). The second step in the harvest sequence involved cutting and double-threshing the remaining plants in each plot. Data were recorded on total aboveground plant weight and yield (adjusted to 13% moisture). Subsample totals were added to plot totals before statistical analyses were performed.

Data on all variables were analyzed using standard ANOVA techniques for a split-plot design. Significant differences because of defoliation level, simulation methods, or their interaction were isolated with orthogonal treatment comparisons. Results of the main plot experiment, the general effects of defoliation levels on soybean morphology, development, and yield components, are discussed in Part II. The present paper explores the effects of simulation methods, and their components, technique and temporal pattern, on soybean response to defoliation.

RESULTS AND DISCUSSION

Vegetative Morphology and Development

Simulation methods generated differential responses to defoliation in three aspects of plant morphology: remaining leaf area, height, and lodging susceptibility (Table 1). In contrast, no differences in vegetative or reproductive development were detected between defoliation techniques, temporal patterns, or the interaction of these components.

Presence of significant differences in leaf area suggested that either defoliation levels were not equivalent between simulation methods or soybeans responded differentially to simulation methods. Measurements taken immediately after defoliation indicated that equivalent reductions in leaf area were achieved by simulation methods in all years. However, in 1982, defoliation levels varied slightly, although nonsignificantly, between simulation methods. These differences were accentuated through time and exceeded the $p = 0.05$ significance level at 4 weeks postdefoliation. Consequently, these late-season differences in leaf area reflected an initial difference in defoliation level plus the contribution of the simulation method. In both 1980 and 1982, significant differences in leaf area developed within the weeks following defoliation. In 1980, punch-defoliated plants possessed 5.5% less leaf area than pick-defoliated plants 18 days after defoliation. Similarly, in 1982, punch-defoliated plants possessed 5.3% less leaf area 31 days after defoliation. Temporal pattern produced fewer differences than defoliation technique. One-day defoliation in 1982 left plants with 7.0% more leaf area than defoliation over time (insect or equal temporal patterns) (Table 1). In all years, no differences in

Table 1. Comparison of simulation methods in their effects on soybean vegetative morphology and lodging susceptibility

	Leaf area (cm^2/plant)[a]			Height (cm)[a]			Lodging susceptibility[b]	
	1980	1981	1982	1980	1981	1982	1980	1982
Simulation methods[c]								
Pick x insect-model	1222	1092	1197	118.2	103.8	125.8	2.88	1.33
Pick x equal	--	1091	1214	--	104.5	124.2	--	1.50
Pick x one-day	1155	1106	1310	119.2	103.3	126.0	3.13	1.40
Punch x insect-model	1155	1097	1149	113.4	100.4	119.2	2.50	1.25
Punch x equal	--	1088	1163	--	102.6	118.6	--	1.20
Punch x one-day	--	1073	1216	--	105.4	122.8	--	1.45
Component								
Technique[d]								
Pick	1222	1096	1240	118.2	103.9	125.3	2.88	1.41
Punch	1155	1086	1176	113.4	102.8	120.2	2.50	1.30
Temporal pattern[e]								
Insect-model	1222	1095	1173	118.2	102.1	122.5	2.88	1.29
Equal	--	1090	1190	--	103.6	121.4	--	1.35
One-day	1155	1090	1263	119.2	104.4	124.4	3.13	1.43
Statistical significance[f]								
Technique	*	n.s.	*	*	n.s.	*	*	n.s.
Temporal pattern	*	n.s.	*	n.s.	*	*	n.s.	n.s.

[a]Measured 18-31 days after defoliation.

[b]Measured on a 1-5 scale where 1 = upright, 5 = horizontal.

[c]See text for description of simulation methods. Means are generated across all defoliation levels and represent soybean response to ca. 120 GCW larval equivalents per m of row.

[d]Means for technique in 1980 included only the insect-model temporal pattern.

[e]Means for temporal pattern in 1980 included only the pick technique.

[f]An asterisk indicates the occurrence of one or more significant ($p<0.05$) orthogonal comparisons between treatments.

leaf area were detected between plots defoliated by insect or equal defoliation.

Appearance of method differences in leaf area could involve lower leaf abscission or upper leaf development and expansion. In general, defoliation technique seemed to alter rates of lower leaf abscission. For example, in 1981, pick-defoliated plants retained more lower leaves and, thus, greater lower leaf area than punch-defoliated plants. Similarly, in 1982, punch-defoliated plants lost more leaf area (201 cm^2) in the four weeks following defoliation than pick-defoliated plants (163 cm^2). Temporal patterns elicited a response in lower-leaf abscission only during 1980. Insect defoliation led to greater leaf retention than one-day defoliation. In contrast to effects on leaf retention, defoliation techniques did not affect upper leaf development or expansion. Temporal patterns produced clear-cut, but temporary, effects on upper leaf expansion. Soybean plants defoliated on one day possessed greater leaf area in upper nodes than plants defoliated over time in both 1980 and 1981. Within 18 days in 1980 and 19 days in 1981, differences caused by temporal pattern had disappeared. Temporary suppression of upper leaf expansion reflected the timing and severity of defoliation under each temporal pattern. Both insect-model and equal defoliation subjected soybean to ca. 8 days of defoliation stress before the one-day defoliation was imposed.

Soybean height, like leaf area, responded to both defoliation technique and temporal pattern (Table 1). Unlike the transitory effects on leaf area, both components of the simulation methods produced persistent height differentials. One-day defoliation resulted in taller plants than

either insect or equal defoliation in both 1980 and 1981. Presumably, increased plant height, like greater upper leaf expansion, reflected the delayed onset of defoliation stress in the one-day temporal pattern. Punch-defoliated plants exhibited shorter stature than pick-defoliated plants in 1980 and 1982. Because development of mainstem nodes was unaffected by defoliation, height differentials apparently resulted from shortened internodes. Once defoliation was completed, height differentials remained fairly constant, suggesting no prolonged method effects on stem elongation.

Lodging susceptibility exhibited a mixed relationship with simulation methods. Presumably, the height differentials just discussed could contribute to differences in lodging susceptibility. In only one year, 1980, were differences in lodging scores detected between simulation methods (Table 1). Pick-defoliated plants lodged more severely than punch-defoliated plants. This trend parallelled the height differentials measured in 1980. A similar trend was observed in 1981, but a thunderstorm severely lodged all plants before the pattern could be measured. No differences between simulation methods emerged in 1982.

Yield and Yield Components

Despite equivalent defoliation levels, simulation methods produced differences in yield or yield components each year (Table 2). Total plant and seed weights responded to both components of the simulation method, technique and temporal pattern. Apparent harvest ratio (yield/total plant dry weight) was relatively unaffected by simulation methods. Because simulation methods did not alter the basic partitioning of photosynthate between structural and reproductive components, seed and total plant weights

Table 2. Soybean yield and yield components after defoliation by various simulation methods

	Yield (g/plant)			Pods per plant		
	1980	1981	1982	1980	1981	1982
Simulation method[a]						
Pick x insect-model	14.18	14.25	12.33	25.95	25.26	25.81
Pick x equal	---	13.58	12.21	---	23.93	25.70
Pick x one-day	13.80	14.18	12.88	24.34	25.46	27.18
Punch x insect-model	13.45	14.39	11.77	25.93	27.01	25.71
Punch x equal	---	13.98	11.56	---	25.33	25.49
Punch x one-day	---	14.02	12.36	---	25.45	26.37
Components						
Technique[b]						
Pick	14.18	14.00	12.47	25.95	24.88	26.23
Punch	13.45	14.13	11.90	25.93	25.93	25.86
Temporal Pattern[c]						
Insect-model	14.18	14.32	12.05	25.95	26.14	25.76
Equal	---	13.78	11.89	---	24.63	25.60
One-day	13.80	14.10	12.62	24.34	25.46	26.78
Statistical significance[d]						
Technique	*	n.s.	*	n.s.	*	n.s.
Temporal pattern	n.s.	*	*	*	*	n.s.

[a]See text for description of simulation methods. Means are generated across all defoliation levels and represent soybean response to ca. 120 GCW larval equivalents per m of row.

[b]Means for technique in 1980 included only the insect-model temporal pattern.

[c]Means for temporal pattern in 1980 included only the pick technique.

[d]An asterisk indicates the occurrence of one or more significant ($p<0.05$) orthogonal comparisons between treatments

Seeds per plant			Seed size (g/100 seeds)		
1980	1981	1982	1980	1981	1982
66.99	60.47	64.48	21.18	22.53	19.09
---	57.09	63.25	---	22.80	19.27
62.94	61.23	67.11	21.98	22.15	19.20
66.47	63.68	63.70	20.26	21.62	18.46
---	63.09	63.52	---	21.21	18.17
---	61.85	65.17	---	21.69	18.92
66.99	59.60	64.95	21.18	22.49	19.19
66.47	62.87	64.13	20.26	21.51	18.52
66.99	62.08	64.09	21.18	22.08	18.78
---	60.09	63.39	---	22.01	18.72
62.47	61.54	66.14	21.98	21.92	19.06
n.s.	*	n.s.	*	*	*
*	n.s.	n.s.	n.s.	n.s.	n.s.

exhibited similar responses to simulation methods. Therefore, the following discussion centers on yield, although it also applies to total plant weight.

Both defoliation technique and temporal pattern of defoliation influenced yield (Table 2). During 1982, pick-defoliated soybeans outyielded punch-defoliated soybeans. A similar pattern emerged in 1980, but no differences between defoliation techniques were detected in 1981. One-day defoliation produced plants with consistently greater yields than equal defoliation. Insect-model defoliation, however, produced variable results. During 1981, insect-model defoliation, like one-day defoliation, reduced yield less than equal defoliation. In contrast, in 1982, insect-model defoliation generated a yield response similar to equal defoliation. This vacillation in soybean response to temporal pattern may involve the timing of defoliation relative to moisture stress and soybean reproductive phenology. Soybean plants were under severe moisture stress during defoliation in 1981 (Part II). Under these conditions, insect-model defoliation, which had its greatest impact near the end of the defoliation period (days 11-12), produced a response similar to one-day defoliation, which also had its impact near the end of the defoliation period (day 8). In contrast, under the normal moisture conditions of 1982 (Part II), insect-model defoliation produced a response similar to equal defoliation.

Yield can be envisioned as the product of several components which are sequentially determined as the season progresses. This concept is expressed in the equation:

$$\text{Yield} = \text{nodes/plant} \times \text{pods/node} \times \text{seeds/pod} \times \text{seed size} \qquad (1)$$

Analysis of these yield components provides clues on how simulation methods affected yield (Table 2). Surprisingly, each aspect of the simulation method, technique and temporal pattern, primarily affected different yield components.

Temporal pattern differentially affected pod and seed number per plant (Table 2). Because no effects of defoliation on total nodes per plant or on seeds per pod were detected, these differences in pod and seed number primarily reflected variation in the ability to set new pods or to maintain existing pods. Generally, differences between temporal patterns in pod and seed number were not consistent between years. In 1980, one-day defoliation produced the lowest pod and seed numbers. In 1981, for reasons discussed earlier, equal defoliation reduced pod numbers relative to insect-model and one-day defoliation. Although nonsignificant in 1982, defoliation over time (insect-model and equal temporal patterns) resulted in fewer pods and seeds than one-day defoliation. In each year, the effects of temporal pattern on yield were directly attributable to effects on pod set and abortion. Moreover, within the plant, these effects were limited to nodes with defoliated leaves (typically nodes 4-9). Temporal pattern did not significantly affect other yield components. Because soybeans are beginning to set pods at the end of the defoliation period, these results on pod number are consistent with the transitory impact of temporal pattern on leaf area.

Defoliation technique primarily produced differences in seed size. Each year, punch-defoliated plants produced consistently lighter seeds than pick-defoliated plants (Table 2). This difference in seed size accounted for the yield discrepancies observed between defoliation techniques in all years except 1981. During 1981, the difference in seed size was offset by

an opposite trend in pod number. Punch-defoliated plants possessed more pods than pick-defoliated plants. Thus, in 1981, pick defoliation reduced pod-set or caused more pod abortion than punch defoliation. Later in the season, because source size (leaf area) per plant was equivalent (Table 1), pick-defoliated plants compensated for reduced pod and seed number through increased seed size. This finding suggested that differences in seed size during 1980 and 1982 also might involve source-sink relationships.

Seed size depends on the relative size, proximity, and capacities of sources (leaves) and sinks (seeds) during later reproductive stages. Variation in seed size between defoliation techniques could result from differences in: (1) available source size (cm^2 of remaining leaf area) per seed, (2) photosynthetic capacity per unit of leaf area, or (3) a combination of these factors. This concept is expressed in the equation:

$$\text{Seed size (g/seed)} = \text{source size (cm}^2\text{/seed)} \times \text{source capacity (g/cm}^2\text{)} \quad (2)$$

Results of the analysis of these components appear in Table 3.

Temporal patterns affected neither source size or source capacity (Table 3). Similarly, defoliation techniques did not produce detectable differences in source capacity. Thus, different simulation methods did not seem to alter the basic ability of soybean leaves to assimilate carbon dioxide and export photosynthate to developing seeds. This finding is consistent with the overall effects of defoliation techniques on another basic physiological process, transpiration (Part I).

Differences in seed size between defoliation techniques were consistently related to changes in source size per seed (Table 3). Previously,

Table 3. Source size (leaf area) per seed (cm^2/seed) and source capacity (g/cm^2) of soybean after defoliation by several simulation methods

	Source size			Source capacity (x 100)		
	1980	1981	1982	1980	1981	1982
Simulation methods[a]						
Pick x insect-model	17.57	18.09	18.71	1.215	1.315	1.035
Pick x equal	---	19.21	19.34	---	1.255	1.018
Pick x one-day	18.26	18.08	19.60	1.217	1.288	0.989
Punch x insect-model	16.31	17.22	18.05	1.257	1.326	1.037
Punch x equal	---	17.32	18.30	---	1.295	1.001
Punch x one-day	---	17.39	18.70	---	1.326	1.019
Components						
Technique[b]						
Pick	17.57	18.46	19.22	1.215	1.286	1.014
Punch	16.31	17.31	18.35	1.257	1.316	1.019
Temporal pattern[c]						
Insect-model	17.57	17.66	18.38	1.215	1.321	1.036
Equal	---	18.27	18.82	---	1.275	1.010
One-day	18.26	17.74	19.15	1.217	1.307	1.004
Statistical significance[d]						
Technique	*	*	*	n.s.	n.s.	n.s.
Temporal pattern	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

[a]See text for description of simulation methods. Means were generated across all defoliation levels and represent soybean response to ca. 120 GCW larval equivalents per m of row.

[b]Means for technique in 1980 included only the insect-model temporal pattern.

[c]Means for temporal pattern in 1980 included only the pick technique.

[d]An asterisk indicates the occurrence of one or more significant ($p<0.05$) orthogonal comparisons between treatments.

we demonstrated that yield differences between defoliation techniques were primarily caused by variation in seed size. Consequently, yield differences between defoliation techniques reflected relative changes in source size per seed. Punch defoliation consistently produced less source size per seed than pick defoliation. Differences in source size per seed may develop through changes in leaf area or in pod and seed set. Data on punch and pick defoliation suggested contributions by both factors. As mentioned previously, punch-defoliated plants tended to maintain less total leaf area and, in particular, less lower leaf area than pick-defoliated plants. Whether this reduction in leaf area is sufficient to consistently explain reduced source size per seed is unknown. Defoliation techniques also seemed to exert differential effects on the ability of sobyeans to set and maintain pods and seeds. In 1981, punch-defoliated plants set and maintained more pods and seeds than pick-defoliated soybeans, despite equivalent amounts of leaf area. This finding suggests that pick defoliation may interfere with pod set or may increase pod abortion compared to punch defoliation.

Relative Importance and Effects on Economic Injury Levels

During the previous paragraphs, we presented evidence that simulation methods elicited differential growth and yield responses to defoliation. These differences between methods, although detectable, may not be sufficiently large to significantly alter the basic relationships between soybean variables and defoliation level. To assess the relative importance of simulation methods, the proportions of experimental variation (R^2) explained by each factor (defoliation level, defoliation technique, temporal

pattern of defoliation) and their interactions were examined (Table 4). With the exception of seed size, defoliation level clearly explained a majority of the variation, accounting for 3 to 11 times the variability explained by either defoliation technique or temporal pattern of defoliation. Defoliation technique, as discussed previously, played a dominant role in seed size variability. Importantly, for all variables, simulation methods did not alter the basic relationship with defoliation level (Part II) but did alter the magnitude of the response.

The goal of studies utilizing damage simulation methods is to approximate the relationship between yield loss and insect damage. Subsequently, this relationship can be used to calculate economic injury levels (EILs). To further assess their relative impact, yield-loss estimates (g/larval equivalent) were derived for each simulation method, defoliation technique, and temporal pattern using regression analyses (Table 5). EILs were calculated from the average yield-loss estimate for 1981 and 1982 using the procedures outlined by Hammond and Pedigo (1982). Yield-loss estimates from 1980 were excluded from EIL comparisons because all simulation methods were not used in that year. Based on current control costs ($16.68/ha for carbaryl aerially applied at 1.25 a.i./ha, efficacy ca. 90%) and current soybean prices ($0.27/kg) in Iowa, a gain threshold of 61.8 kg/ha was used in the EIL calculations.

Although technique and temporal pattern accounted for a small proportion of experimental variability in yield (Table 5), both components of the simulation method distinctly affected yield-loss estimates and subsequent EILs. Differences between defoliation techniques and temporal patterns were consistent with previously discussed trends. Within each component

Table 4. Relative importance (R^2) of defoliation level, simulation method, and their interaction in explaining experimental variability (1981-1982)[a]

Source of variation	Seed yield				Pods per plant		Seeds per pod		Seed size	
	Plot		Subsample							
	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982
Defoliation level	.219	.237	.457	.378	.233	.352	.196	.333	.280	.175
Simulation method	.063	.109	n.s.	.062	.104	n.s.	.113	n.s.	.227	.221
Technique	n.s.	.047	n.s.	.028	.036	n.s.	.066	n.s.	.183	.154
Temporal pattern	.060	.045	.020	.034	.049	n.s.	n.s.	n.s.	n.s.	n.s.
Technique x temporal pattern	n.s.	.017	n.s.	n.s.	n.s.	n.s.	.030	n.s.	.042	.037
Level x method	.125	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.109	n.s.

[a]Data for 1980 excluded because not all simulation methods were used.

Table 5. Yield-loss estimates (g/larval equivalent) and economic injury levels (larval equivalents/m of row) for soybean defoliated by several methods simulating first-generation green cloverworm defoliation

Simulation method[a]	Yield-loss estimates				Economic injury level[d]
	1980	1981	1982[b]	Average[c]	
Pick x insect-model	-0.141	-0.174	-0.164	-0.169	27.87
Pick x equal	---	-0.219	-0.118	-0.169	27.87
Pick x one-day	-0.121	-0.121	-0.142	-0.132	35.68
Punch x insect-model	-0.163	-0.167	-0.204	-0.186	25.32
Punch x equal	---	-0.285	-0.239	-0.262	17.97
Punch x one-day	---	-0.175	-0.190	-0.183	25.73
Averages					
Defoliation technique					
Pick	---	-0.166	-0.170	-0.168	28.03
Punch	---	-0.225	-0.257	-0.241	19.54
Temporal pattern					
Insect-model	---	-0.177	-0.211	-0.194	24.27
Equal	---	-0.248	-0.199	-0.224	21.02
One day	---	-0.154	-0.180	-0.167	28.20
Overall	-0.160	-0.202	-0.236	-0.219	21.50

[a] See text for description of simulation methods.

[b] Values are least squares means from an analysis of covariance. Analysis was designed to eliminate suspected differences in defoliation level between simulation methods.

[c] Average based on values from 1981 and 1982.

[d] EILs calculated from average yield-loss estimates.

of the simulation method, measures taken to achieve greater fidelity to insect damage resulted in greater yield-loss estimates and lower EILs. For example, punch defoliation produced greater yield-loss per larval equivalent and lower EILs than pick-defoliation. The punch technique was developed by Poston and Pedigo (1976) to mimic the tattering effect of natural insect defoliation in soybean. Similarly, defoliation over time (insect-model and equal temporal components) produced greater yield-loss per larval equivalent and lower EILs than one-day defoliation. One-day defoliation was originally developed to simulate hail defoliation (Kalton et al., 1949). Subsequently, Poston and Pedigo (1976) and Hammond and Pedigo (1982) developed a more realistic temporal pattern for insect defoliation using an insect consumption model. Thus, the most commonly used simulation method, pick defoliation on one day, produced the lowest yield-loss estimates and the highest EILs (Table 5). In contrast, punch defoliation following the equal temporal pattern produced the highest yield-loss estimates and lowest EILs. The remaining simulation methods gave comparable yield-loss estimates and EILs. These simulation methods included: picking leaflets over time (insect-model and equal temporal patterns), punching holes on one-day, and punching holes following the insect-model temporal pattern. If the trend towards greater realism proves valid, then the punch x insect-model method, and equivalent methods, intuitively should exhibit greater fidelity to insect defoliation.

The use of simulation methods in soybean defoliation studies is based on the premise that only the quantity of leaf area removed is important in the plant response to defoliation. A corollary of this premise is the assumption that simulation methods will not alter soybean response to

defoliation. The results of this study clearly demonstrate that the choice of the simulation method can affect soybean response to defoliation and, ultimately, the derived yield-loss relationship and calculated EILs. Clearly, further experimentation that compares simulation methods and actual insect defoliation in their effects on soybean growth and yield is required. The results of our study indicate that all variables need not be measured in this fidelity experiment. Noting the differences between methods in their effects on remaining leaf area, pod and seed numbers, seed size, and yield, future studies on fidelity of simulation methods should focus on these variables.

A lack of definitive studies on simulation fidelity does not negate the value of simulation studies. Indeed, simulation methods provide the only reliable and feasible means of approximating the damage-loss relationship. Furthermore, we found that each simulation method generated the same fundamental response to defoliaton, differing only in the magnitude of this response. Therefore, if future studies legitimize one or more simulation methods, then our data will provide a means of calibrating existing EILs derived with other simulation methods. Pending future studies on damage fidelity, simulation methods should be selected with caution and designed to closely mimic the natural phenology and within-plant distribution of insect defoliation.

PART IV. DISTRIBUTION OF LEAF AREA AND YIELD WITHIN SOYBEAN PLANTS AFTER SIMULATED INSECT DEFOLIATION

ABSTRACT

Insect pests, such as the green cloverworm (GCW) (*Plathypena scabra* [F.]), commonly defoliate soybean. Soybean yield responses to defoliation are well-documented, but little information exists on how insect defoliation alters yield distribution within the soybean plant. Using the GCW in Iowa soybean as a model system, the distribution of remaining leaf area and yield within soybean after simulated insect defoliation was examined. Secondarily, the effects of natural lodging on defoliated and undefoliated plants was investigated. Simulated GCW defoliation at stages R2 to R3 linearly reduced leaf area within nodes 6-11. Compensation through lower-leaf retention and upper-leaf expansion was limited (<18%). Defoliation reduced lodging susceptibility. At harvest, yield reductions primarily occurred at nodes 4-9. Within this zone, defoliation primarily reduced pod and seed number and secondarily reduced seed size. The downward shift in defoliation effects on yield by two nodes seemed related to translocation patterns. Defoliation reduced source size per seed (cm^2 of leaf area/seed) but soybeans compensated ca. 87% through increased source capacity (g/cm^2 of leaf area). Lodging interacted with defoliation to alter yield distribution within the plant. Lodging also interacted with defoliation to partially offset potential yield reductions from defoliation.

INTRODUCTION

During a normal growing season, soybeans (*Glycine max* [L.] Merr.) suffer defoliation caused by a number of natural agents. Growth and yield responses to defoliation have been investigated for hail (Kalton et al., 1949; Camery and Weber, 1953; Fehr et al., 1977), insects (Todd and Morgan, 1972; Thomas et al., 1974; Hammond and Pedigo, 1982) and disease (Lockwood et al., 1977). These studies have focused on the defoliation-damage syndrome at the plant and plot level with little consideration of how defoliation alters yield distribution within the plant.

The distribution of yield and its components within soybean after insect defoliation reflects the interaction of several factors. First, insect damage is normally stratified within the soybean canopy. For example, the green cloverworm (*Plathypena scabra* [F.]), a serious lepidopteran pest of soybean, primarily defoliates soybean in the upper 1/2 to 1/3 of the soybean canopy (Pedigo et al., 1973). Consequently, such defoliation alters the distribution of leaf area within the plant. Second, because light is principally absorbed at the periphery of the canopy (Sakamoto and Shaw, 1967), insect defoliation in the upper canopy can increase light penetration into the middle and lower canopy. If leaves at these nodes can respond to increased levels of photosynthetically-active radiation, yield at these nodes could increase. Third, seed yield at a given node is affected by translocation of photosynthate within the plant (Thrower, 1962; Blomquist and Kust, 1971; Stephenson and Wilson, 1977). Finally, defoliation reduces lodging susceptibility (Kalton et al., 1949; Higgins et al., 1983). Because lodging reduces yield (Woods and Swearingin, 1977), decreased

lodging susceptibility of defoliated plants may partially offset the relative effects of defoliation (Higgins et al., 1983). Lodging affects yield distribution because it disrupts an optimal display of leaf area, alters the light regime of lower and middle leaves, and possibly increases plant susceptibility to disease. Individually and collectively, these four factors can change the distribution of yield and yield components within the soybean plant.

Continuing progress towards comprehensive economic decision levels for insect pests, which incorporate abiotic and biotic factors that affect the damage-loss relationship, requires an understanding of how plants respond to insect injury (Poston et al., 1983). Gathering basic data on how defoliation translates into yield losses also can provide the information necessary to generate defoliation submodels for soybean growth models such as SOYMOD (Meyer et al., 1979) or SOYGRO (Wilkerson et al., 1983). Therefore, the objectives of this research were: (1) to quantify the distribution of leaf area, yield, and yield components within the soybean plant; (2) to determine the effects of defoliation on the distribution of these plant variables; and (3) to investigate the effects of natural lodging on the distribution of yield.

MATERIALS AND METHODS

Experiments were conducted from 1980 to 1982 on a Coland clay loam soil (fine-loamy, mixed, mesic, Cumulic Haploquoll) near Ames, IA. Soybeans (var. Amsoy 71) were overseeded into 76-cm wide rows on 22 May 1980, 20 May 1981, and 2 June 1982. Within three days after emergence, each row was hand-thinned to a density of 30 plants per m of row in 1980 and 1981, and 26.7 plants per m of row in 1982.

Defoliation by natural green cloverworm populations in Iowa soybean served as the model for our experimental system. A comprehensive hypothesis of green cloverworm population dynamics in Iowa is provided by Pedigo et al. (1983) and Buntin and Pedigo (1983). Two larval generations occur in Iowa. The first attacks soybean during stages R2 to R3 (Fehr and Caviness, 1977), and the second defoliates soybean during stages R5 to R6. Typically, the green cloverworm only poses an economic threat during the first generation (Pedigo et al., 1983). Therefore, this study explored soybean response to simulated GCW defoliation during soybean stage R2. The steps taken to insure synchrony of natural and experimental systems are outlined in Part II.

Soybean response to defoliation was evaluated using a split-plot design. Main plots specified levels of defoliation and subplots designated various simulation methods used to impose this defoliation. The main plots, each measuring 25 m x 5 rows, were arranged in a randomized complete block design with four replications in 1980 and 1981, and five replications in 1982. Each year, main-plot treatments simulated GCW defoliation in incremental densities of "larval equivalents." A larval equivalent was

defined as the total consumption of one GCW larvae from egg hatch to pupation (54.3 cm^2) (Hammond et al., 1979b). Defoliation levels varied between years, depending on the predefoliation leaf area index (LAI). Simulated GCW densities, expressed as GCW larval equivalents per m of row, included: 1980 - 0, 60, 120, and 180; 1981 - 0, 80, 120, and 160; and 1982 - 0, 60, 120, and 180.

Subplots, each three rows x 3 m, were located within each main plot on the basis of stand (30 or 26.7 plants per m of row) and uniform plant morphology. Subplot treatments designated the combination of defoliation technique (the way in which leaf area was removed) and temporal pattern of defoliation (the distribution of damage through time) used to defoliate the center row of each subplot. The number of subplot treatments varied from three in 1980 to six in 1981 and 1982. These subplot treatments are described in greater detail in Part III. Defoliation treatments were imposed over a 12-day period beginning 14 July 1980, 13 July 1981, and 19 July 1982.

Integrity of defoliation treatments was preserved through several measures. First, to eliminate possible treatment confounding from handling during defoliation, soybeans in all plots were lightly handled each day. Secondly, the outside two rows of each subplot and a 0.5 m buffer at the ends of each subplot were sham-defoliated to a level visually equivalent to the center row. Finally, additional defoliation by natural GCW populations was eliminated through application of the microbial insecticide, *Bacillus thuringiensis* Berliner.

Leaf area distributions were measured on a nodal basis two times following defoliation. The first measurement, occurring 1-5 days after

defoliation, was designed to measure the direct effects of defoliation on leaf area distribution. The second measurement, ranging from 12 to 31 days after defoliation, was designed to assess the indirect effects of defoliation on lower-leaf retention and upper-leaf expansion. Leaf area was measured nondestructively using a LiCor® LI-3000 portable leaf area meter.

At harvest, a subsample of plants was selected from each subplot for determining the nodal distribution of yield and yield components. Subsamples included 6 plants per plot in 1980, 9 plants per plot in 1981, and 15 plants per plot in 1982. Each plant was chosen on a stratified random basis. Positions within each subplot were selected at random and the five-plant grouping nearest each position was examined. The median plant, in stem-base diameter, was chosen for the yield subsample. Atypical plants, such as Y-plants, runts, or severely diseased plants, were not selected. Data collected on a nodal basis from this subsample included: pod number, seed number, pod weight (including seeds), and seed weight. Seed weights were adjusted to 13% moisture before statistical analyses.

Total plant and plot responses to defoliation and simulation methods were analyzed using standard ANOVA techniques for split-plot designs. These results are summarized in Parts II and III. Analysis of leaf area and yield distributions focused solely on the main-plot level. This analysis proceeded in three steps. First, nodal distributions of leaf area, yield, and yield components were analyzed using standard ANOVA techniques for a split-plot design. Significant differences in these variables between defoliation levels served to delimit the nodal boundaries of three zones within the soybean plant: a lower undefoliated zone termed the abscission zone, a middle defoliated zone termed the defoliation zone, and

an upper undefoliated zone called the expansion zone. Second, leaf area, yield, and yield components within these zones were analyzed using standard ANOVA techniques for split-plot designs. Finally, overall relationships between yield components and leaf area were analyzed using polynomial regression techniques.

RESULTS AND DISCUSSION

Analysis of leaf area immediately after defoliation was used to delineate nodes where defoliation significantly reduced leaf area. An example of the nodal distributions of leaf area in defoliated and undefoliated plants is presented in Figure 1. Simulated GCW defoliation significantly reduced leaf area in nodes 7-12 (1980), 6-11 (1981), and 6-11 (1982). Although defoliation was imposed on the upper 1/2 of the soybean canopy at full bloom (R2), subsequent vegetative development relegated this zone to the middle 1/3 of the canopy during beginning seed and full seed (R5-R6). The defoliation zone contained ca. 75-80% of the total leaf area during these later reproductive stages. Leaf area within this zone declined linearly with increasing defoliation levels in all years (Table 1). Maximum defoliation levels, ranging from 160 to 180 GCW larval equivalents per m of row, reduced total leaf area 31% (1980), 28% (1981), and 29% (1982). Leaf area within the defoliation zone decreased 59%, 64%, and 58%, respectively. No direct effects of defoliation were detected outside the middle defoliation zone.

Indirect effects of defoliation on leaf area were detected in the lower undefoliated, or abscission, zone and in the upper undefoliated, or expansion, zone. Defoliation retarded lower-leaf abscission in 1980 (Table 1). A similar trend, although nonsignificant, was observed in 1981. Higgins et al. (1983) also found increased retention of lower leaves by defoliated soybean. Retention of lower leaves presumably resulted from increased penetration of photosynthetically-active radiation (PAR) into the lower canopy after defoliation. Delayed leaf abscission, although

Figure 1. Distribution of leaf area (cm^2/plant) by node of undefoliated soybean and soybean damaged by simulated green cloverworm defoliation (120 larval equivalents per m of row). Asterisks designate nodes with significant reductions in leaf area

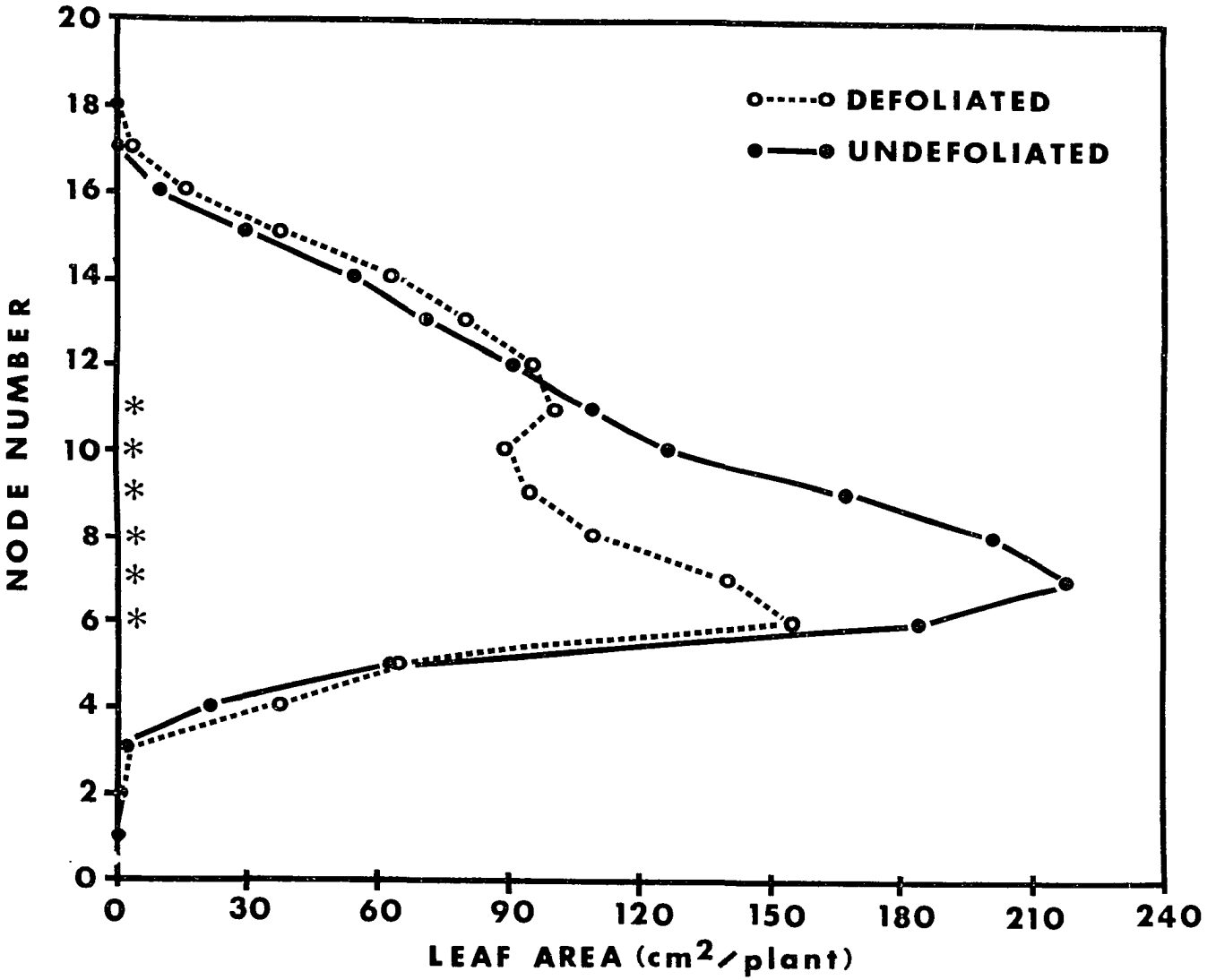

DEFOLIATED
UNDEFOLIATED
NODE NUMBER
LEAF AREA (cm2/plant)
0
2
4
6
8
10
12
14
16
18
20
0
30
60
90
120
150
180
210
240

Table 1. Leaf area (cm^2/plant) in lower abscission, middle defoliation, and upper expansion zones of soybean damaged by simulated green cloverworm defoliation

Zone	1980					1981		
	Date[a]	Intercept[b]	Slope[b]	p[c]	R^2[d]	Date[a]	Intercept[b]	Slope[b]
Lower	2	155	---	n.s.	---	5	111	---
	18	47	+1.67	.004	.416	19	81	+0.77
Middle	2	1148	-8.74	.001	.852	5	975	-7.98
	18	1173	-9.01	.001	.934	19	1000	-8.52
Upper	2	119	---	n.s.	---	5	60	---
	18	212	---	n.s.	---	19	267	+0.68
Total	2	1424	-8.56	.001	.811	5	1132	-7.56
	18	1444	-7.76	.001	.837	19	1345	-7.02

[a]Days after defoliation.

[b]Intercept(a) and slope(b) of linear regression y = a+bx where x = no. GCW larval equivalents per 30 cm of row.

[c]Significance level of linear regression.

[d]Proportion of main plot variability explained by linear regression.

1981			1982			
p[c]	R^2[d]	Date[a]	Intercept[b]	Slope[b]	p[c]	R^2[d]
n.s.	---	5	174	---	n.s.	---
.114	.199	31	52	---	n.s.	---
.001	.854	5	1138	-8.31	.001	.881
.001	.881	31	1104	-8.59	.001	.890
n.s.	---	5	192	---	n.s.	---
.034	.095	31	366	---	n.s.	---
.001	.764	5	1475	-7.37	.001	.580
.001	.729	31	1508	-8.15	.001	.785

detectable, probably contributed little to yield compensation for three reasons. First, defoliation only delayed, but did not prevent, leaf abscission. Second, because of age and acclimation to a low-PAR environment, lower leaves possess relatively low photosynthetic capacities compared to upper leaves (Beuerlein and Pendleton, 1971). Finally, lower leaves seem unable to respond appreciably to changes in the PAR regime by increasing yield (Weil and Ohlrogge, 1976).

Defoliation usually failed to affect upper leaf development and expansion (Table 1). However, in 1981, alleviation of a severe drought at the end of the defoliation period permitted additional vegetative growth. Defoliation, under these conditions, promoted greater expansion and development of upper leaves. The total compensatory response to defoliation, including lower-leaf retention and upper-leaf expansion, offset only 13% (1980), 18% (1981), and 5% (1982) of the defoliated leaf area. Thus, compensation for defoliation initiated at full bloom was limited. This finding agrees with Boote's (1981) contention that leaf-area compensation, or "compensatory regrowth," after defoliation is largely a myth.

Simulated green cloverworm defoliation produced linear reductions in yield (Table 2). Maximum defoliaton levels, ca. 30%, reduced plot yields 8.8% (1980), 11.1% (1981), and 16.8% (1982). An example of the nodal distributions of yield in defoliated and undefoliated soybean is presented in Figure 2. Yield analysis, by node, revealed significant reductions at nodes 4-10 (1980), 5-9 (1981), and 1-9 (1982). These nodes collectively contributed 57-61% of the total yield within undefoliated soybean. Seed weight within this zone declined linearly with defoliation level (Table 2).

Table 2. Yield and yield components in lower undefoliated, middle defoliated and upper undefoliated zones of soybean damaged by simulated green cloverworm defoliation

Zone[a] / Variable	1980 Intercept[b]	1980 Slope[b]	1980 p[c]	1980 R^2[d]	1981 Intercept[b]
Lower[e]					
Yield (g/plant)	0.10	---	n.s.	---	0.55
Pods/plant	0.24	---	n.s.	---	1.06
Seeds/plant	0.53	---	n.s.	---	2.51
Seed size	12.72	---	n.s.	---	22.05
Seeds/pod	1.350	---	n.s.	---	1.997
Middle					
Yield (g/plant)	8.85	-.047	<.001	.770	8.25
Pods/plant	15.85	-.070	<.001	.663	14.67
Seeds/plant	41.37	-.190	<.001	.654	35.16
Seed size (g/100 seeds)	21.47	-.003	.109	.185	23.49
Seeds/pod	2.598	---	n.s.	---	2.428
Upper					
Yield (g/plant)	6.52	---	n.s.	---	6.20
Pods/plant	11.84	---	n.s.	---	11.55
Seeds/plant	30.21	---	n.s.	---	27.90
Seed size (g/100 seeds)	21.82	---	n.s.	---	22.77
Seeds/pod	2.550	---	n.s.	---	2.416
Total					
Yield (g/plant)	15.40	-.044	<.001	.452	15.90
Pods/plant	27.88	-.066	.007	.239	27.77
Seeds/plant	71.67	-.162	.009	.239	66.11
Seed size (g/100 seeds)	21.55	-.015	.183	.118	23.05
Seeds/pod	2.581	---	n.s.	---	2.407

[a]Zone boundaries include:
Lower - 1-3 (1980), 1-4 (1981)
Middle - 4-10 (1980), 5-9 (1981), 1-9 (1982)
Upper - 11-18 (1980), 10-18 (1981), 10-18 (1982).

[b]Intercept (a) and slope (b) in linear regression $y = a+bx$, where x = no. GCW larval equivalents per 30 cm of row.

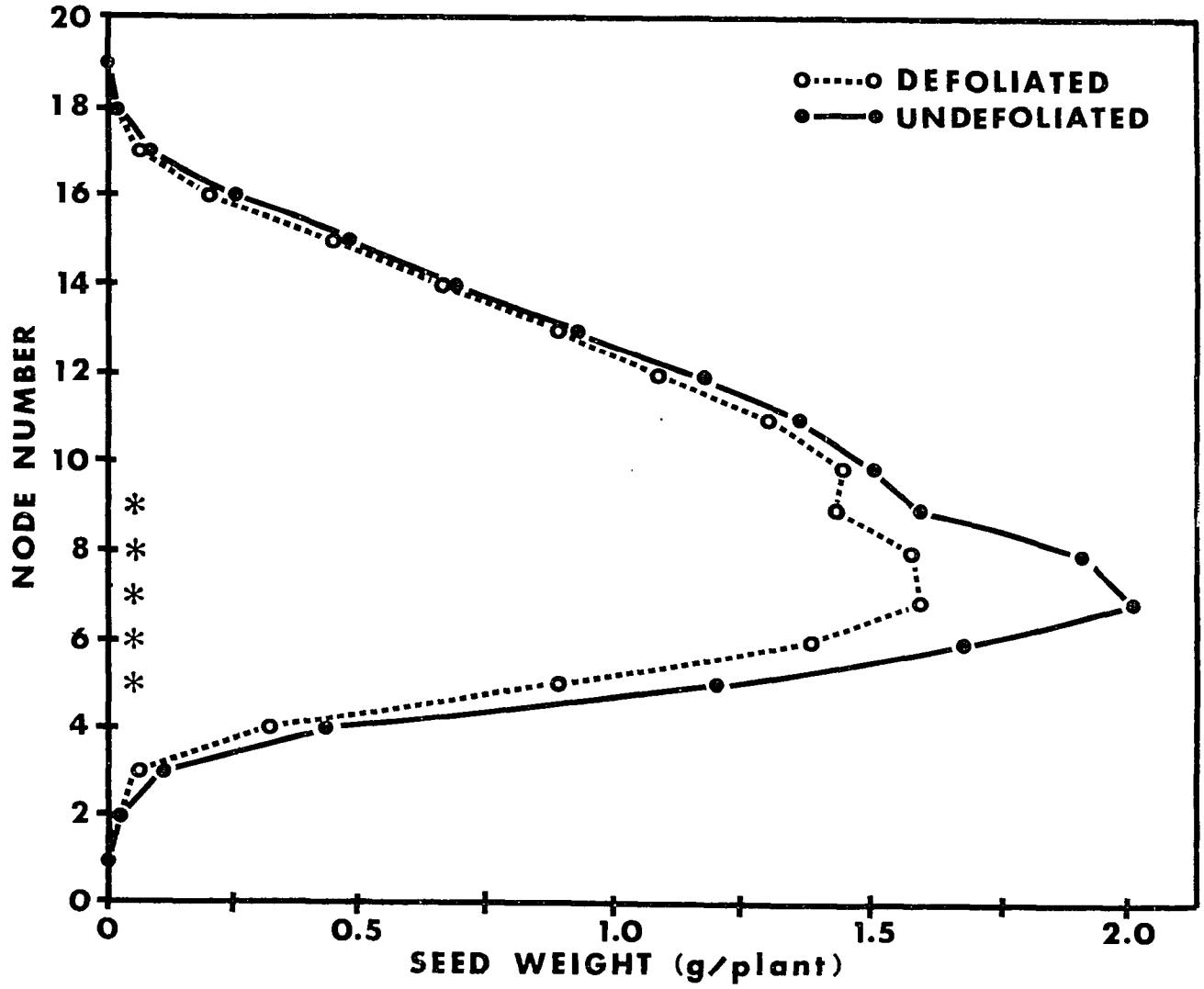
[c]Significance level of linear regression.

[d]Proportion of main plot variability explained by linear regression.

[e]No lower zone was detected in 1982.

1981			1982			
Slope[b]	p[c]	R^2[d]	Intercept[b]	Slope[b]	p[c]	R^2[d]
-.004	.023	.300				
---	n.s.	---				
-.015	.066	.144				
-.048	.029	.218				
---	n.s.	---				
-.037	<.001	.717	8.58	-.055	<.001	.717
-.052	<.001	.593	17.43	-.098	<.001	.768
-.114	.001	.591	43.02	-.241	<.001	.733
-.034	<.001	.727	20.01	-.023	.001	.437
---	n.s.	---	2.472	---	n.s.	---
---	n.s.	---	5.05	---	n.s.	---
---	n.s.	---	11.26	---	n.s.	---
---	n.s.	---	27.75	---	n.s.	---
-0.25	<.001	.491	18.51	-.000	.041	.188
---	n.s.	---	2.462	---	n.s.	---
-.050	.001	.378	14.03	-.052	<.001	.338
-.065	.005	.185	29.20	-.087	<.001	.301
-.134	.017	.149	72.34	-.217	<.001	.272
-.028	<.001	.209	19.45	-.017	.002	.153
---	n.s.	---	2.475	---	n.s.	---

Figure 2. Distribution of yield (g/plant) by node of undefoliated soybean and soybean damaged by simulated green cloverworm defoliation (120 larval equivalents per m of row). Asterisks designate nodes with significant reductions in leaf area


DEFOLIATED
UNDEFOLIATED
NODE NUMBER
SEED WEIGHT (g/plant)
0
2
4
6
8
10
12
14
16
18
20
0
0.5
1.0
1.5
2.0
*
*
*
*
*

In contrast, seed weight within the upper nodes was relatively unaffected by defoliation. Each year, the upper limit of yield reductions occurred two nodes below the upper limit of the defoliation zone (Figures 1 and 2). For example, in 1980, defoliation reduced leaf area at nodes 7-12, whereas defoliation reduced yield at nodes 4-10. Thus, defoliation averaging ca. 32% at these upper two nodes of the defoliation zone failed to produce detectable yield losses. This downward shift in defoliation effects on yield presumably involves translocation patterns within the soybean plant during late reproductive stages (R5-R6).

Soybean leaves during pod-fill predominantly export assimilate to the closest reproductive sinks, the pods at the leaf's axil (Blomquist and Kust, 1971; Stephenson and Wilson, 1977). However, upper leaves also export assimilate to adjacent nodes. Blomquist and Kust (1971) demonstrated a strong phyllotactic relationship in translocation with assimilate primarily exported to leaves two nodes below the source leaf. In contrast, Stephenson and Wilson (1977) reported a weaker phyllotactic relationship. They found that source leaves exported assimilate to leaves within a zone two nodes above and below the source leaf. Regardless of phyllotactic constraints, the potential clearly exists for undefoliated leaves to export assimilate to reproductive sinks at the axils of nearby defoliated leaves. Thrower's (1962) work with soybean during vegetative stages also suggests that defoliation at lower nodes enhances the downward exportation of assimilate from upper undefoliated leaves. The effects of defoliation on translocation during reproductive stages are unknown. Collectively, these previous studies indicate that importation of assimilates from higher undefoliated leaves could offset potential yield reductions at the upper two

nodes of the defoliation zone. Supportive evidence for this hypothesis was obtained by regressing total yield within the zone of yield reduction, typically nodes 4-9, on leaf area remaining within the defoliation zone, typically nodes 6-11. Because of variation in the lower limits of yield and leaf area reductions, the lower limits of both zones were dropped to the cotyledonary nodes for this analysis. Each year, a significant linear regression was obtained. For all years combined, yield was significantly related to remaining leaf area ($p < 0.01$, $R^2 = 0.888$) by the equation:

$$\text{Yield (g)} = 2.19 + 0.0060 * (\text{Remaining leaf area } (cm^2)). \quad (1)$$

This model provided the best explanation, highest R^2, of all models evaluated.

Simulated GCW defoliation produced linear reductions in yield, pod number, seed number, and seed size (Table 2). Because no differences in vegetative development were detected, reduced pod numbers imply that defoliation decreased pod set or increased pod abortion. No apparent effects on seed set were detected because seeds per pod did not vary with defoliation level. Reductions in pod number and, thus, seed number of soybean defoliated at stages R2 and R3 are widely reported (Thomas et al., 1976; Fehr et al., 1977; Hammond and Pedigo, 1982). Similarly, reductions in seed size by defoliation at stages R2 and R3 are widely noted (Kalton et al., 1949; Todd and Morgan, 1972; Hammond and Pedigo, 1982). However, defoliation at these early reproductive stages causes proportionately greater reductions in pod number than seed size (Fehr et al., 1977). Defoliation levels approaching 30% in our study reduced pod and seed numbers 13.4%, while seed size was reduced only 4.3%. Therefore, yield reductions

primarily involved reduction in pod number and, secondarily, decreased seed size. These results agree with Fehr et al. (1977, 1981), who found that percent reduction in seed number exceeded those in seed size for defoliation at all reproductive stages except R6. Thus, defoliation at stages R2 to R3 clearly reduced soybean's ability to set and maintain pods and to fill pods.

Defoliation effects on soybean yield and yield components were primarily confined to the lower half of the soybean canopy (Table 2). Usually, no significant effects on yield or yield components were observed in the upper half of the soybean plant. Only one variable, seed size, was affected throughout the plant in 1981 and 1982. Appearance of this systemic effect may indicate a hormonal response to defoliation. The systemic effect of defoliation on seed size may also involve alteration of translocation patterns. Stephenson and Wilson (1977) reported that the combined translocation of assimilates to pods at the surrounding four nodes, two nodes above and below the source leaf, equalled or exceeded the contribution to pods at the axil of the source leaf in normal undefoliated soybean. Thrower (1962) found that defoliation of lower leaves produced a strong downward flow of assimilates from a source leaf at the expense of translocation to upper leaves. During stages of rapid seed growth, a similar translocation of assimilates from upper undefoliated leaves to pods in the axils of defoliated leaves may occur at the expense of seed size at the upper nodes.

Final seed size depends on the relative size, proximity, and capacities of sources and sinks during pod fill. Variation in seed size after

defoliation could result from differences in: (1) available source size per seed (cm^2 of remaining leaf area per seed); (2) source capacity to fix assimilate (g/cm^2); or (3) a combination of these factors. This concept is expressed in the equation:

$$\text{Seed size (g/seed)} = \text{source size } (cm^2/\text{seed}) \times \text{source capacity } (g/cm^2). \quad (2)$$

Source size per seed declined linearly with increasing defoliation level each year (Table 3). In other words, defoliated plants set more pods per unit of remaining leaf area than undefoliated plants. Assuming equivalent source capacity, reduced seed size would clearly result from this relative decrease in source size per seed. Surprisingly, a further compensatory response to defoliation was observed in source capacity. Source capacity increased linearly with increasing defoliation level (Table 3). Thus, defoliated soybean produced greater yield per unit of remaining leaf area. Increased source capacity of defoliated plants, considering the proportionately greater seed set per unit of leaf area, clearly indicates a dynamic response to greater sink demand. Koller et al. (1970) and Dornhoff and Shibles (1970) have speculated that increased net photosynthesis during pod fill may be a response to increased demand for assimilates by the developing seeds. If net assimilation rates are related to, or controlled by, the relative supply and demand for assimilates, then defoliation, which decreases relative source size per seed, should increase the relative demand for assimilate. Consequently, defoliation should increase source capacity. Thorne and Koller (1974) found that soybean (var. Amsoy 71) reponded to

Table 3. Source size per seed (cm^2/seed) and source capacity (g/cm^2) of soybean after simulated green cloverworm defoliation

Year	Linear regression equation	p[a]	R^2[b]
	Source size		
1980	Y = 20.46 - 0.085 * (GCW)[c]	32.19	.708
1981	Y = 20.46 - 0.072 * (GCW)	16.26	.590
1982	Y = 21.13 - 0.063 * (GCW)	18.72	.554
	Source capacity (x 100)		
1980	Y = 1.052 + 0.00483 * (GCW)	39.93	.747
1981	Y = 1.183 + 0.00338 * (GCW)	7.47	.372
1982	Y = 0.930 + 0.00229 * (GCW)	7.73	.345

[a]Significance level of linear regression.

[b]Proportion of main-plot variability explained by the regression.

[c]Defoliation level expressed as green cloverworm larval equivalents per 30 cm of row.

increased sink demand by increasing source-leaf photosynthesis, carbohydrate formation, and translocation.

Lodging susceptibility decreases after defoliation (Kalton et al., 1949; Fehr et al., 1977). Higgins et al. (1983) suggested that lodging forms an integral component of the defoliation syndrome. Lodging is known to reduce the yield of undefoliated soybean (Woods and Swearingin, 1977). Delayed onset and severity of lodging after defoliation imply that lodging effects on yield will be reduced by defoliation. Lodging produces proportionately greater yield losses in undefoliated soybean than in defoliated soybean (Johnston and Pendleton, 1968). Consequently, decreased lodging susceptibility may partially offset the potential yield reductions caused by defoliation (Higgins et al., 1983).

Severe natural lodging of our plots at the end of defoliation in 1982 provided an opportunity to evaluate the relative effects of lodging on defoliated and undefoliated soybean. Lodging scores (1-5 scale), taken four days after defoliation ended, verified a decrease in lodging susceptibility after defoliation. Lodging scores declined linearly with increasing defoliation level ($p < 0.001$, $R^2 = 0.694$):

$$\text{Score} = 2.24 - 0.023 \times (\text{GCW larval equivalents per 30 cm of row}). \quad (3)$$

At harvest, the proportion of severely-lodged plants (lodging score > 3) also declined linearly with increasing defoliation level ($p < 0.01$, $R^2 = 0.222$):

$$\text{Proportion} = 0.379 - 0.0018 \times (\text{GCW larval equivalents per 30 cm of row}). \quad (4)$$

Severely-lodged plants possessed ca. 50% of "normal" yield (Table 4). This reduction in yield included both the physiological and mechanical effects of lodging and indirect effects, such as increased disease susceptibility. Just as importantly, this yield reduction also reflected the tendency for higher-density, lower-yielding plants to lodge more readily than lower-density, higher-yielding plants within the same plot. Consequently, yield differences cannot be solely attributed to lodging. However, these data provided excellent indications of the relative effects of lodging on defoliated and undefoliated plants.

Lodging produced a distinct alteration in the distribution of pods and yield within the plant. The yield contribution of each node, expressed as a proportion of the maximum yielding node, is presented in Figure 3 for normal to slightly-lodged plants and for severely-lodged plants. Lodging, unlike defoliation, reduced yields proportionately more within the upper half of the soybean canopy (nodes 10-18). Severely-lodged plants produced 56% of "normal" yield in nodes 1-9, but only 41% of "normal" yield in nodes 10-18. Observations at harvest suggested that severe lodging reduced pod set and possibly seed size at the upper nodes. Severely-lodged plants produced 61% of the pods produced by slightly-lodged plants in nodes 1-0, but only 41% of the pods in nodes 10-18. Thus, the relative yield reductions observed in the upper nodes primarily reflected decreased ability to set and maintain pods. An additional facet of the lodging syndrome, which may have affected yield distribution, was increased disease incidence in lodged plants. Many of the severely-lodged plants exhibited disease symptoms that were tentatively diagnosed as stem canker (*Diaporthe phaseolorum* [Cke. and Ell.] Sacc. var. *caulivora* Heatow and Caldwell).

Table 4. Yield and yield components of undefoliated and defoliated soybean classified by lodging score into upright (score <3) and lodged (score >3) plants[a]

Zone / Variable	Upright				Lodged			
	Check	Defoliated[b]	Δ%	p[c]	Check	Defoliated[b]	Δ%	p[c]
Lower (nodes 1-9)								
Yield (g/plant)	10.35	7.57	-26.9	***	5.78	4.25	-26.5	***
Pods (no./plant)	20.71	15.31	-26.1	***	12.38	9.77	-21.1	***
Seeds (no./plant)	51.73	38.34	-25.9	***	29.67	23.26	-21.8	***
Seeds/pod	2.545	2.489	-2.2	n.s.	2.393	2.385	-0.3	n.s.
Seeds size (g/100 seeds)	20.03	19.70	-1.6	*	19.45	18.22	-6.3	**
Middle (nodes 10-13)								
Yield (g/plant)	5.04	4.65	-7.7	*	1.96	2.15	+9.7	n.s.
Pods (no./plant)	10.28	9.63	-6.3	*	4.25	4.99	+17.4	*
Seeds (no./plant)	26.13	24.27	-7.1	**	10.32	12.21	+18.3	*
Seeds/pod	2.540	2.521	-0.7	n.s.	2.421	2.438	+0.7	n.s.
Seed size (g/100 seeds)	19.26	19.19	-0.4	n.s.	18.95	17.60	-7.1	**
Upper (nodes 14-18)								
Yield (g/plant)	2.44	2.29	-6.1	n.s.	0.91	0.78	-14.3	n.s.
Pods (no./plant)	5.69	5.28	-7.2	n.s.	2.65	2.34	-11.7	n.s.
Seeds (no./plant)	14.05	13.15	-6.4	n.s.	5.66	5.00	-11.7	n.s.
Seeds/pod	2.526	2.466	-2.4	n.s.	2.098	2.068	-1.4	n.s.
Seed size (g/100 seeds)	17.32	17.41	-0.5	n.s.	16.27	15.21	-6.5	n.s.

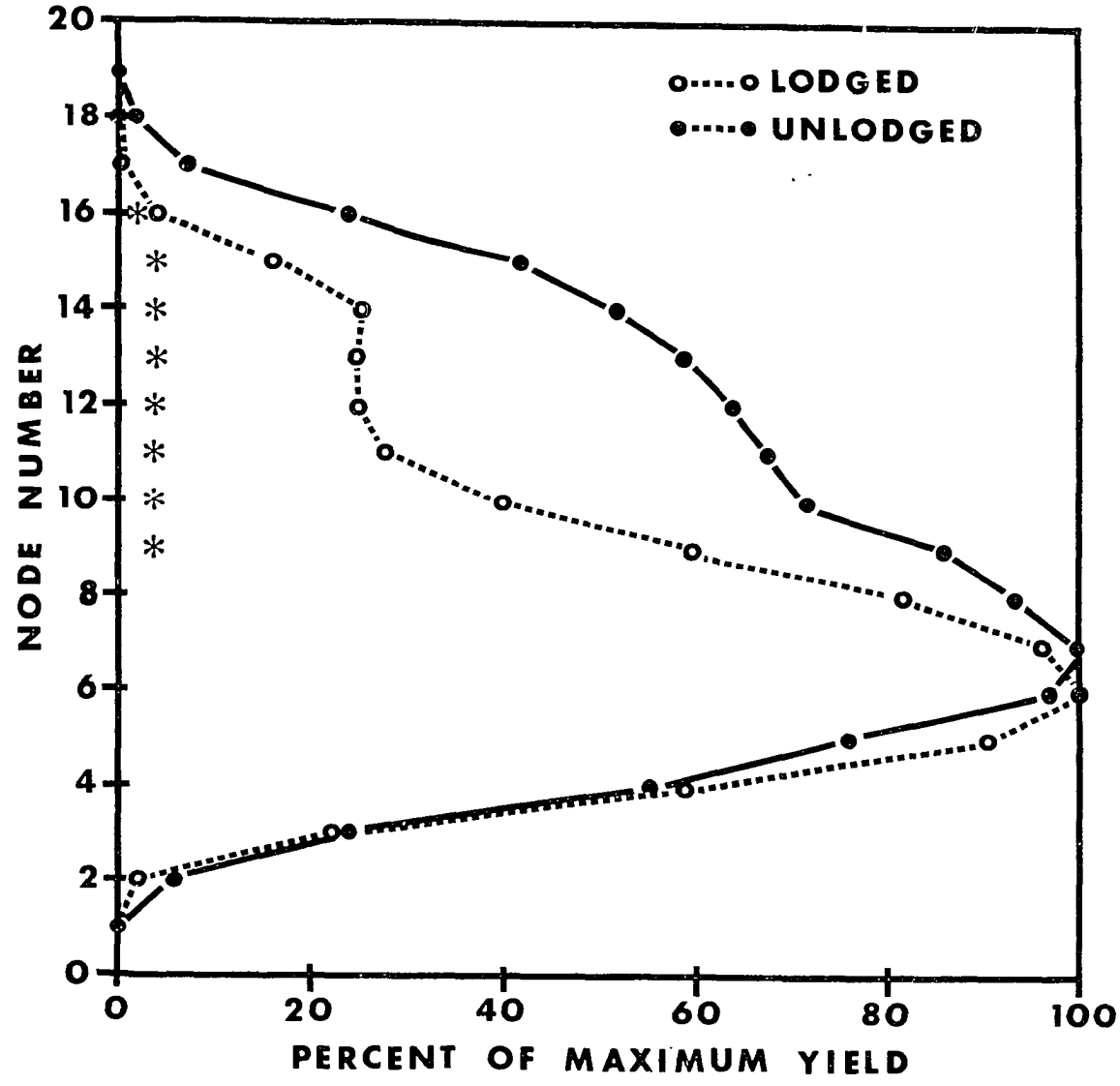
Total								
Yield (g/plant)	17.83	14.51	-18.6	***	8.65	7.18	-17.0	*
Pods (no./plant)	36.68	30.22	-17.6	***	19.28	17.10	-11.3	*
Seeds (no./plant)	91.91	75.76	-17.6	***	45.65	40.47	-11.3	n.s.
Seeds/pod	2.504	2.506	+0.1	n.s.	2.358	2.361	-0.1	n.s.
Seed size (g/100 seeds)	19.41	19.15	-1.4	*	18.97	17.73	-6.6	**

[a]Lodging rated on a 1-5 scale with 1 = upright, 5 = horizontal.

[b]Average of all defoliaton levels, corresponding to ca. 120 GCW larval equivalents per m of row.

[c]Significance of t-test between undefoliated and defoliated plants: * - $0.01<p<0.05$, ** - $0.001<p<0.01$, *** - $p<.001$, n.s. - not significant.

Figure 3. Yield contribution of each node, expressed as a percent of the maximum yielding node, in severely-lodged (lodging score >3) and upright to slightly-lodged (lodging score <3) soybean. Asterisks designate nodes with significant differences in yield proportions


o····o LODGED
●····● UNLODGED
NODE NUMBER
PERCENT OF MAXIMUM YIELD
0
2
4
6
8
10
12
14
16
18
20
0
20
40
60
80
100

The effects of defoliation on yield and yield components of slightly-lodged and severely-lodged soybean are presented in Table 4. As discussed previously, these data were gathered from naturally-lodged plants. Lower-yielding plants in greater density areas of each plot tended to lodge more readily than higher-yielding plants in lesser density areas of the plot. Therefore, the relative effects of defoliation (Δ%) provide a more accurate interpretation of the interaction between defoliation and lodging than absolute values (Table 4). Lodging beginning at stage R3 interacted with defoliation in both the lower zone (nodes 1-9), where defoliation primarily affected yield and yield components (Table 2), and in the middle zone (nodes 10-13). Within these two zones, defoliation effects on pod and seed number were lessened by lodging. In contrast, defoliation effects on seed size were accentuated by lodging in all zones. Within the lower zone, these interactive effects balanced to produce comparable yield responses to defoliation in both slightly- and severely-lodged plants. In the middle zone, the interactive effects on pod set outweighed the interactive effects on seed size. Consequently, yield, pod number, and seed number in lodged plants increased with increasing defoliation level. In contrast, these variables decreased with increasing defoliation level in slightly-lodged plants.

The pattern of interaction between defoliation and lodging suggests an impact on sink formation (pod set) and the subsequent ability to meet sink demand. Defoliation delays the onset and severity of lodging. For lodging beginning at R3, this delay would permit pod set to proceed normally in defoliated plants, reflecting only the effects of defoliation. However, in undefoliated plants, severe lodging at R3 would disrupt optimal leaf

display in addition to other physiological and mechanical effects of lodging. Thus, lodging would enhance any defoliation effects on the soybean's ability to set and maintain pods. Later, as leaf display was rearranged in undefoliated plants and the defoliated plants progressively lodged, undefoliated plants could meet sink demand better than defoliated plants. Thus, defoliation reductions in seed size would be enhanced by lodging. This hypothesis is consistent with observed trends in pod and seed number within the lower and middle zones and in seed size throughout the plant (Table 4).

Despite interactive effects of defoliation and lodging on pod set and pod fill, yield responses to defoliation were comparable between slightly-lodged and severely-lodged plants (Table 4). For example, moderate defoliation levels (120 GCW larval equivalents per m of row) reduced yields of slightly-lodged plants 17.6% and yields of severely-lodged plants 17.5%. Thus, considering the entire plant, no interactive effects between defoliation and lodging were detected. However, when considering the entire plot, interactive effects may occur because the proportion of severely-lodged plants varies with defoliation level. Defoliated plots tend to contain fewer severely-lodged, lower-yielding plants than undefoliated plots (equation 4). The impact of this interactive effect on yield was evaluated using an analysis of covariance. By utilizing the proportion of severely-lodged plants as a covariate, yields for each defoliation level were adjusted to a common proportion of severely-lodged plants. Yield for undefoliated soybean increased 4.3%, from 886.6 g/3.0 m to 925.1 g/3.0 m, when variation in the proportion of severely-lodged plants was removed. Yield loss (g per GCW larval equivalent) increased 34.3%, from -0.260 to -0.349.

These results strongly support the contention by Higgins et al. (1983) that lodging can partially offset potential yield reductions from defoliation.

PART V. THE USE OF MORTALITY ESTIMATES FROM INSECT LIFE TABLES IN DERIVING ECONOMIC THRESHOLDS

INTRODUCTION

Insect pest management seeks to maintain pest populations at densities that avoid economic damage with minimal cost to the producer and minimal adverse impact to the environment. Stern et al. (1959) pioneered the concepts of economic damage, economic-injury level, and economic threshold which underlie current pest management programs. By integrating agricultural economics with biology of the crop-pest system, pest management promotes the efficient use of management resources. Since their original definition, ambiguous usage and the proliferation of related terms (e.g., action threshold, decision level, decision level threshold) has clouded the meaning and philosophical orientation provided by economic-injury level and economic threshold concepts. Yet, these concepts remain viable and should serve as the focal point for every pest management program.

Before initiating a discussion of these concepts, a review of their original definitions by Stern et al. (1959) is appropriate. The economic injury level is defined as the "lowest population density that will cause economic damage." EILs vary from area to area and from season to season; therefore, use of the "lowest" density implies an economically conservative approach. The economic threshold is defined as "the density at which control measures should be determined to prevent an increasing pest population from exceeding the economic-injury level." This definition also is conservative, because economic damage is avoided by incorporating the time delay between detection of a pest problem and the attainment of efficacy by the control measure. Thus, the economic threshold reflects the logistical problems of implementing a management decision.

Researchers have approached the derivation of ETs for specific crop-pest situations in two completely different approaches, empirically and theoretically. Both approaches attempt to improve management efficiency by eliminating the unnecessary use of insecticides while preventing economic damage. The empirical approach seeks the solution to a management problem without investigating the crop-pest interaction. Typically, various combinations of control measures, chemical or biological, and arbitrary thresholds are evaluated for their effectiveness (e.g., Cancelado and Radcliffe, 1979; Sears et al., 1983). Optimal combinations are selected on a cost/benefit basis. Although this research does produce a management solution, it does not generate information about the crop-pest interaction. Consequently, each new management situation (e.g., new variety, control measure, resistant biotype) requires a new series of experiments. In contrast to the empirical approach, the theoretical approach relies heavily on research of the crop-pest interaction to derive, first, the EIL, and second, the ET. Classically, this approach involves a determination of the damage potential per individual. These data then are incorporated with a damage-loss relationship to calculate the EIL (e.g., Stone and Pedigo, 1972; Berry and Shields, 1980; Kolodny-Hirsch and Harrison, 1980). ETs subsequently may be derived to reflect management logistics. The EILs and ETs derived from this approach are largely theoretical because they incorporate the full damage potential of each pest individual. However, pest populations rarely attain their full damage potential because of extensive mortality by natural agents (predators, parasitoids, diseases, nematodes, and the abiotic environment). Consequently, this approach, by assuming 100% survivorship, overestimates the contribution of each pest individual

and, therefore, underestimates ETs for field situation. This shortcoming can be overcome with further research on pest population dynamics. Estimates of mortality then can be incorporated into ET calculations (e.g., Oseto and Braness, 1980).

Current approaches in deriving ETs have largely ignored the potential contribution of natural control. This trend is unfortunate, considering the emphasis that Stern et al. (1959) placed on natural control and its importance to integrated control of insect pests. Natural mortality agents can play an important role in reducing the damage potential of pest populations. Incorporating estimates of natural control into ETs should promote a more efficient use of production resources. Therefore, we propose a method whereby mortality estimates can be incorporated into ET calculations and demonstrate its applicability to the management of the green cloverworm (*Plathypena scabra* [F.]) in Iowa soybean.

GENERAL THEORY

The purpose of the EIL and derived ET is to provide, within managerial constraints, advance warning of economic damage. The EIL and ET are designed to render a management decision based on the potential for future damage. In its simplest form, survivorship is assumed to be 100% and damage potential can be directly related to insect numbers. In its more advanced form, survivorship estimates are used to modify the potential for future damage and future damage potential is directly related to "damage equivalents." A damage equivalent is defined as the damage potential of one pest individual, assuming 100% survivorship. The derivation of damage equivalents for each damaging stage of the pest requires data on three components: (1) stage-specific estimates of survivorship (S_i), (2) stage-specific estimates of damage potential (D_i), and (3) a risk factor (α).

During the following discussion, the pest species is assumed to have n damaging stages and a total damage potential, assuming 100% survivorship, of TD. The future damage (FD) from an individual at stage i is the summed product of survivorship in future stages (S_i) and its damage potential during those stages (D_i):

$$FD = \sum_{j=i}^{n} S_j D_j .$$

Similarly, the realized damage of an individual at stage i is the summed product of survivorship in past stages (1.000) and damage potential during those stages (D_i):

$$RD = \sum_{j=1}^{i} D_j.$$

Thus, the expectation of total damage from an individual at stage i (ED) is the sum of its realized damage (RD) plus its future damage (FD):

$$ED = RD + FD.$$

Because of mortality, a pest individual only reaches a portion of its total damage potential (TD). The proportion of the total damage potential expected from an individual at stage i is its damage equivalency (DEQ):

$$DEQ = ED/TD.$$

The damage potential of a population subsequently can be calculated from a table of these damage equivalencies. The damage potential of a sample (DP) is the summed product of the abundance of each stage in the sample (A_i) and the damage equivalency of each stage (DEQ_i):

$$DP = \sum_{i=1}^{n} A_i DEQ_i.$$

In a pest management program, damage potential (total damage equivalents) can be used in place of insect numbers in sampling programs (e.g., sequential sampling).

The stage-specific estimates of natural mortality used in the previous equations can be obtained through the preparation of life tables for the insect pest. The development and use of insect life tables are discussed more thoroughly by Morris and Miller (1954), Ives (1964), and Harcourt

(1969). The insect life table provides a valuable tool for studying the population dynamics of an insect and for quantitatively assessing the impacts of mortality factors on different life stages. A series of life tables provides an idea of the variability in stage-specific mortality and may serve to elucidate the underlying causes of population fluctuations. Estimates of variability in stage-specific survivorship can be used to minimize the risk associated with using these estimates. Ideally, survivorship values should be chosen which minimize the risk of damage exceeding expectations while maximizing the role of natural mortality. These goals can be accomplished by establishing upper confidence limits on survivorship. This upper confidence limit can be calculated from mean stage-specific survivorship ($\bar{x}_i$) using estimates of the variance in stage-specific survivorship (s_i) in the following formula:

$$S_i = \bar{x} + t_{(2\alpha, n-1)}(s_i/\sqrt{n}),$$

where α is the desired risk level, t is Student's t, and n is the number of estimates of survivorship from the life table studies. This value of S_i can then be substituted for S_i in the previous equations. The result is a table of damage equivalents that conservatively estimates natural mortality based upon the desired level of risk (α). It should be noted that the overall level of risk (R), viz., the probability that survivorship exceeds this conservative estimate for all life stages, is:

$$R = (\alpha)^x, \text{ where } x = \text{number of life stages.}$$

AN EXAMPLE WITH THE GREEN CLOVERWORM IN IOWA

The green cloverworm is a serious, but sporadic, defoliator of soybeans in Iowa. Two larval generations attack soybean each year with the first defoliating during full bloom (R2) and the second defoliating during late pod and early seed (R4 and R5). Results of partial life table studies for the larval stages (Pedigo et al., 1983) have revealed two types of population configurations. During an endemic configuration, neither larval generation exceeds the economic threshold, but the second generation is much larger than the first. During an outbreak configuration, the first generation may exceed the economic threshold. An outbreak of the fungus *Nomuraea rileyi* (Farlow) typically reduces larval densities in the second generation well below the economic threshold. Population configurations and the potential for economic damage during the first generation seem related to the abundance of immigrating GCW. A more detailed hypothesis of GCW population dynamics in Iowa soybean is presented by Buntin and Pedigo (1983) and Pedigo et al. (1983).

Development of EILs and ETs for the GCW in Iowa soybean has followed the theoretical approach outlined earlier. EILs were first presented by Stone and Pedigo (1972). These authors combined experimental data on foliar consumption with earlier data on soybean response to simulated hail defoliation (Kalton et al., 1949) to calculate EILs. Later, refinement of these EILs was deemed necessary because simulated hail defoliation produced damage atypical of GCW defoliation in its appearance, distribution in the canopy, and temporal pattern. Development of a GCW leaf-consumption model (Hammond et al., 1979b) and a new defoliation technique, punching holes in

leaves (Poston and Pedigo, 1976), resulted in a more appropriate simulation method. Subsequent studies have utilized this simulation method to establish EILs for first generation GCW larvae (Hammond and Pedigo, 1982; Higgins et al., 1984; Part II). Continuing progress towards comprehensive EILs and ETs (Poston et al., 1983) has produced EILs reflecting moisture stress (Part II). Each of these studies used simulation methods to impose defoliation in terms of larval damage equivalents. One larval equivalent was defined as the total consumption of a GCW larva from egg hatch to pupation (54.3 cm^2) (Hammond et al., 1979b). Thus, the resulting EILs are equivalent to a field situation in which survivorship is 100%. Data from a recent life-table study (Pedigo et al., 1983) reveal that GCW populations suffer extensive mortality. For example, survivorship from egg to adult averaged only 0.021% during generation I and only 0.010% during generation II. This example illustrates the extent of GCW mortality and suggests that current EILs, which ignore this mortality, may result in unnecessary treatments.

The sporadic nature of GCW outbreaks and their economic consequences has promoted extensive research on GCW life history, population dynamics, and bioeconomics in soybean. This research has generated the data necessary to calculate damage equivalencies for each stage of larval development. Hammond et al. (1979a) developed a thermal unit model for describing the development of the GCW from egg to adult. Hammond et al. (1979b) modelled the leaf consumption of GCW larvae as a function of thermal unit accumulations. Jointly, these models provided the first data requirement, estimates of stage-specific consumption. Data for the second requirement,

estimates of stage-specific survivorship, were found in partial life table studies by Bechinski and Pedigo (1983b) and Pedigo et al. (1983). Pedigo et al. (1983) grouped larval stages as follows: small (instars 1 and 2), medium (instars 3 and 4), and large (instars 5, 6, and 7 (if present)). Both life-table studies estimated stage abundance using Southwood's (1978) area under the curve method. Under certain conditions, this method reliably estimates numbers present at the midpoint of the stage. Thus, the survivorship estimates of Pedigo et al. (1983) and Bechinski and Pedigo (1983b) apply from the midpoint of a stage to the midpoint of the succeeding stage. Consequently, the stage limits in Tables 1-3 reflect this midpoint-to-midpoint interval.

Summary data necessary to calculate damage equivalents for each life-stage of the green cloverworm are presented in Tables 1 and 2. The risk factor ($\alpha = 0.05$) was used in calculating the upper limit of the confidence interval for each stage-specific estimate of survival. Because reliable data is lacking on the survivorship from mid-egg to mid-small larvae, a survivorship value of 1.000 was assumed in the calculations. The damage equivalents of each larval stage (excluding the egg to small larval interval) are presented in Table 3 for generations I and II. Estimates of stage-specific survivorship during generation I were not significantly different between population configurations. Therefore, a single value was obtained for survivorship and for damage equivalency. In contrast to generation I, survivorship in generation II was significantly lower during outbreak configurations than during endemic configurations. These differences in survivorship are reflected in the resulting values for damage equivalents.

Table 1. Thermal unit limits, realized damage (p_i), and current consumption (c_i) of green cloverworm life stages

Life stage	Thermal unit limits[a]	Realized damage (cm^2)[b]	Current stage consumption (cm^2)
Egg ⟶ small larva	61.5, 196.5	0	0.42
Small ⟶ medium larva	196.5, 337	0.42	2.26
Medium ⟶ large larva	337, 517	2.68	21.94
Large larva ⟶ pupa	517, 753	24.62	29.28

[a]Based on Hammond et al. (1979a).

[b]Based on Hammond et al. (1979b).

Table 2. Average stage-specific survivorship by generation of green cloverworm life-stages during endemic and outbreak population configurations [calculated from Pedigo et al. (1983) and Bechinski and Pedigo (1983b)]

Life stage	Generation I[a]	Generation II	
		Endemic	Outbreak
Egg ⟶ small larva	NA[b]	NA	NA
Small ⟶ medium larva	0.8128 (0.9245)[c]	0.8775 (0.9274)	0.5087 (0.6939)
Medium ⟶ large larva	0.3531 (0.4186)	0.3050 (0.3990)	0.0793 (0.1448)
Large larva ⟶ pupa	0.5445 (0.6714)	0.7790 (0.9642)[d]	0.2840 (0.4692)[d]

[a]Stage-specific survivorship did not differ between population configurations during generation I.

[b]Accurate estimates of egg survivorship are not available.

[c]Values in parentheses represent the upper limit of the 90% confidence interval on average survivorship.

[d]No estimates of variance were possible from Bechinski and Pedigo (1983), so a maximum variance equal to the maximum variance of all stages was assumed in calculating the upper limit of the 90% confidence interval.

Table 3. Damage equivalence, by generation, of green cloverworm life stages during endemic and outbreak population configurations[a]

Life stage	Generation I[b]	Generation II	
		Endemic	Outbreak
Small ⟶ medium larva	.577	.727	.348
Medium ⟶ large larva	.580	.731	.361
Large larva ⟶ pupa	.815	.973	.706

[a]1 damage equivalent equals the total consumption one GCW larva from egg hatch to pupation (543 cm^2).

[b]Stage-specific survivorship and, thus, damage equivalence did not differ significantly between population configurations during generation I.

The field use of these damage equivalents is simple and straightforward. An example of a sequential decision plan for first and second generation GCW is presented in Table 4. This plan is developed from the formula (Iwao, 1975):

$$T_0 = qm_0 + t\sqrt{qf(m_0)},$$

where T_0 = upper and lower limits of the confidence interval for the cumulative number of larval damage equivalents, q = number of 60-cm plant shake samples, m_0 = critical mean density of larval damage equivalents, t = Student's t-statistic, and $f(m_0)$ = sampling variance expressed as a function of the mean. Based on Bechinski et al. (1983), the function $s^2 = 0.9890\bar{x}^{1.2183}$ was substituted for $f(m_0)$ in the previous equation. The t statistic was set at 1.64 (i.e., 10% probability level). For generation I, 13.5 was used for m_0 (Part II), whereas, for generation II, 24 was used for m_0. Bechinski et al. (1983) outline the execution of the

Table 4. Sequential decision plans for green cloverworm (GCW) larval management in soybeans

n^b	Cumulative total no. of GCW larval equivalents[a]									
	Soybean stage R2-R3[c]					Soybean stage R4-R5[d]				
	<			>		<			>	
1	Noneconomic populations	--	Continue sampling	--	Treatment required	Noneconomic population	--	Continue sampling	--	Treatment required
2		--		--			--		--	
3		17		64			52		92	
4		22		86			73		119	
5		28		107			94		146	
6		33		129			116		172	
7		39		150			138		198	
8		44		172			160		224	
9		50		193			182		250	
10		55		215			204		276	

[a] See text for details on calculating larval equivalents.

[b] n = Number of 60-cm plant shake samples

[c] Limits for R2-R3 (full bloom to early pod) calculated using an EIL of 13.5 larval equivalents per 60 cm of row (Part II).

[d] Limits for R4-R5 (late pod to early seed) from Bechinski et al. (1983).

sequential decision plan. Only one difference is involved when damage equivalents are used rather than raw insect numbers. At the end of each sample, the larval counts, by stage, must be converted to larval equivalents. For example, assume that a sample, taken during generation I, contained 8 small larvae, 4 medium larvae, and 2 large larvae. The total number of larval equivalents would be 8(.577) + 4(.580) + 4(.815), or ca. 10.2. After each sample, the procedure would be repeated and Table 4 consulted for a decision regarding the cumulative number of larval equivalents. If no decision is reached within 10 samples, sampling should be reinitiated in three days.

Incorporating survivorship estimates into ETs represents a theoretical advance in the ET concept. This approach restores an emphasis on the role of natural control. It is hoped that the use of these refined ETs will prevent the unnecessary use of insecticides and, thus, promote a more efficient use of crop production resources. The value of this approach will be limited to those species on which a life table can be constructed.

SUMMARY AND CONCLUSIONS

Soybean response to simulated green cloverworm (GCW) defoliation was investigated in several experiments from 1980 to 1983. The primary goals of this research were: (1) to assess the fidelity of simulation methods to actual insect defoliation for a basic physiological process, transpiration; (2) to determine if soybean response to defoliation varies between simulation methods; and (3) to elucidate the general effects of defoliation on soybean growth, development, yield, and yield components.

Water loss from potted soybean after defoliation by simulation methods and actual insects (green cloverworm, cabbage looper) demonstrated significant, but transitory, differences during the first 16 hours. These differences seemed related to the "hole" characteristics produced by each type of defoliation. Total water loss over a three-day period did not differ significantly between simulation and actual insect defoliation. Therefore, both simulation methods, punching holes in leaflets and picking entire leaflets, produced acceptable fidelity in soybean water-loss to actual insect defoliaton.

Various simulation methods produced different effects on soybean growth, development, and yield but did not affect basic physiological processes. Transitory, minor differences in water-loss were detected during the first 16 hours after defoliation, but no differences were found in subsequent measurements or in total water loss. Therefore, simulation methods did not affect the transpirational function of remaining leaf tissue. Similarly, the ability of remaining leaf tissue to produce seed yield, as measured by source capacity (g/cm^2 of remaining leaf area) did not differ

between simulation methods in any year.

Simulation methods elicited significantly different responses to defoliation. Each component of a simulation method, technique (the way in which leaf area is removed) and temporal pattern (the distribution of defoliation through time), affected remaining leaf area, height, yield, and yield components. Punch-defoliated plants possessed less leaf area, height, and yield than pick-defoliated plants. One-day defoliation resulted in more leaf area, taller plants, and greater yields than either insect-model or equal defoliation. Yield differences between simulation methods primarily reflected the effects of temporal pattern on pod and seed number and the effects of technique on seed size. Differences in seed size between punch and pick defoliation were related to differences in source size (cm^2 of remaining leaf area) per seed. These differences in source size per seed presumably resulted from increased lower-leaf abscission by punch-defoliated plants and reduced pod set (or increased pod abortion) by pick-defoliated plants. Yield differentials between simulation methods were sufficiently large to significantly affect yield-loss estimates and economic-injury levels (EILs). The most commonly used simulation method, pick defoliation on one day, gave the least yield reductions and the highest EILs. In contrast, punch-defoliation following the equal temporal pattern generated the greatest yield reductions and highest EILs. The remaining four simulation methods elicited similar yield reductions and produced equivalent EILs. These results demonstrated that simulation methods can affect soybean response to defoliation. Therefore, simulation method should be selected with caution and emphasis should be placed on realistically simulating the appearance and spatial and temporal patterns of

insect defoliation. Further experimentation is required to elucidate which simulation methods demonstrate acceptable fidelity to actual insect defoliation.

Simulated GCW defoliation at full-bloom (R2) produced linear reductions in leaf area, height, and lodging susceptibility. Defoliation directly reduced leaf area in nodes 6-11 in most years. Indirect effects of defoliation on lower-leaf abscission and upper-leaf expansion were detected. These compensatory responses, however, were transitory and limited, replacing less than 18% of the leaf area lost to defoliation. Despite defoliation exceeding 30%, vegetative and reproductive phenology was not disrupted. Lodging susceptibility decreased inversely with defoliation level. This reduction in susceptibility presumably reflected both decreased stature and reduced leaf area exposed to the winds' force.

Simulated GCW defoliation also produced significant yield losses, primarily through reduced pod and seed numbers and, secondarily through decreased seed size (weight per seed). Each year, yield declined linearly with increasing defoliation level. Yield reductions were usually observed in nodes 4-9. This reflects a downward shift of two nodes from the reductions in leaf area. Presumably, this downward shift involves the downward translocation of assimilates from upper undefoliated leaves. Defoliation reduces source size (cm^2 of remaining leaf area) per seed, but soybeans compensated ca. 87% through increased source capacity (g/cm^2 of leaf area). Lodging interacted with defoliation to alter yield distribution within the plant. Lodging also interacted with defoliation on a plot basis, because the proportion of severely-lodged, poor yielding plants decreased with defoliation. When this difference in the proportion of severely-lodged

plants was removed with an analysis of covariance, the slope of the damage-loss relationship increased 34%. This finding conclusively supports the concept that subsequent lodging can partially offset the potential yield reductions caused by defoliation.

Using the damage-loss relationships quantified in this experiment, the EIL for first generation GCW larvae was established at 23 larval equivalents per m of soybean row. Past research has demonstrated that the damage-loss relationship is accentuated by moisture stress. Therefore, comprehensive EILs, which reflect seasonal rainfall variation, also were derived. Field use of these EILs is fully conservative, because equating living larvae with larval equivalents implies an assumption of 100% survivorship. Natural mortality, however, is extensive. Consequently, a general theory on incorporating survivorship information into economic threshold calculations was developed. Applicability of this concept, including its use in pest management programs, was demonstrated using the GCW in Iowa.

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